

BULLETIN OF THE RESEARCH COUNCIL OF ISRAEL

Section B ZOOLOGY

Bull. Res. Council. of Israel. B. Zoology

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LETTER TO THE EDITOR

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DR. H. LISSNER'S STUDY OF THE BIOLOGY OF *ACANTHOBRA TERRAE-SANCTAE* IN LAKE TIBERIAS

H. STEINITZ

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INTRODUCTION

A short time after the death of Dr. H. Lissner* in 1951, his notes concerning *Acanthobrama terrae-sanctae* were entrusted to the present writer with the understanding that he edit them, mindful of the aim which Dr. Lissner set for himself when he studied this fish. *A. terrae-sanctae* was known, under the name of the Tiberias sardine, to be one of the most important of the fishes of Lake Tiberias from an economic point of view. For many years the population of this fish had been extensively exploited. The question had finally arisen whether the fishing left enough of a stock to guarantee replacement at the same time as assuring optimal yields. It was evident that when official regulations for the fishing of *A. terrae-sanctae* should be promulgated, they should be based on sound knowledge of its bionomics. However, all that was known of its biology was based on occasional observations and the experience fishermen had gained during years of commercial fishing. A long-range scientific study of the fish had never been made. Dr. Lissner, charged by the authorities with carrying out a comprehensive survey of the Tiberias sardine, at once set out to discharge his obligations with untiring enthusiasm, relying on his vast experience in active fisheries research over 25 years.

A. terrae-sanctae is one of the two species of this genus so far known from this country. It has been found in Lake Tiberias as well as in Lake Huleh and in the Jordan River (Steinitz 1953). It appears that in both these lakes it lives side by side with *A. lissneri* Tortonese (1952). But whereas their relative numbers in Lake Huleh were unknown, it soon became obvious that in Lake Tiberias *A. lissneri* was a relatively rare species and was in any case of no economic importance. On the other hand, *A. terrae-sanctae* is, in Lake Tiberias, a largely pelagic fish. Shoaling and migrating in big shoals at certain times, and perhaps even most of the time, are among its outstanding biological properties. Migrations towards the spawning sites at least have been observed to occur regularly. Spawning takes place in the shallow water of the beach region. There eggs are found fastened to the surface of hard

* Late Director of the Caesarea Sea Fisheries Research Station (Division of Fisheries, Ministry of Agriculture).

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objects, such as pebbles and the like. In accordance with their pelagic habits, these fish are largely plankton feeders (Komarovskiy 1952).

The exceptional position of the fish which Dr. Lissner was about to investigate necessitated the most careful planning. The working plan eventually produced not only took account of everything known so far, but was from the outset organised in a manner which allowed for adjustments as new problems made their appearance. Since the systematics of the species was at that time being revised (Steinitz 1952) and much taxonomic information was still needed, a detailed examination of certain structural features of *A. terrae-sanctae* had been included in Dr. Lissner's research plan. However, only the true Tiberias sardine was considered, and the Huleh population was excluded from the study.

The execution of the plan was started in the autumn of 1948. Dr. Lissner had to work under the most trying circumstances owing to the political situation prevailing by then. Numerous interruptions of the study were forced upon him. He did not know how many years he would have to proceed before something conclusive could be achieved. And when, after almost two years, his own health began to fail, he was sure that several years would have to be added to make the cycle complete. Indeed, the material collected was incomplete, but Dr. Lissner believed until shortly before his death that he might be able to carry on and even to conclude the work. This, however, he was prevented from doing.

The notes that were left by him very vividly reflect his own judgment. Several points of the original plan were evidently investigated to his own satisfaction: results are summarised and statistics calculated to the finish. This will be seen in detail in Part 2 (section 1 and 2) of this paper. But with regard to numerous other problems, treated in Part 1 and Part 3, for instance, several attempts were made to summarise the computations. Subsequently they were abandoned, new data were gathered, and the whole considered anew and again left open for more study. Thus, very different stages of progress were attained in regard to different problems. All in all, there was a wealth of information before us, but it was extremely difficult to put it to the proper use. There was no text whatsoever except for a few words among many thousands of numerical notations. Field work on *A. terrae-sanctae* was kept up for several months* after Dr. Lissner's death. Data from this period have been included in this account and treated just as Dr. Lissner's own data.

Since every detail of publishing Dr. Lissner's results was left to this writer's discretion, it was up to him to choose between a mere condensation of statistical data into as many tables as feasible on the one hand, and some kind of account of the life history of *A. terrae-sanctae* as it emerged from the observations, always relying on the data collected by Dr. Lissner, on the other. It is hoped that the decision favouring the latter alternative comes closer to what Dr. Lissner had set out for.

* All observations indicated as after February, 1951, are to be credited to Dr. Lissner's co-workers.

The present author accepts full responsibility for omissions and for the selection of data. He also has a great measure of responsibility regarding the comments made in the course of the following paragraphs, and for the conclusions drawn. It must further be understood that even the presentation of statistical details involved this writer's judgment. Wherever he thought it necessary, special explanations of the procedure have been included.

1. Material and Sampling

[illegible]

size and distribution of samples. Each black square represents approximately 30 fish and each black and white square approximately 15 fish

Number of fish measured during four periods of study

1. October 1948 to January 1949	484
2. September 1949	16
3. March to May 1950	218
4. February to July 1951	504
	1222

The treatment of biological periods by the combination of figures is prevented by the same basic inadequacy of the material. In the decisive winter season, which comprises the months of spawning in December observations are wanting. Merely summing the 312 observations made during the critical months of January, February and March conveys an entirely misleading impression, since the contributing months are of three different years. This implies so much discontinuity of biotic and abiotic factors of the lake environment that conclusions from such combinations are hardly justified.

Other limitations to analysis resulted from the lack of notes which might have indicated Dr. Lissner's methods of sampling. Thus, the present writer was confronted by considerable difficulties in his task of formulating conclusions from the material before him.

2. Size and Growth

Length measurements were made to the nearest 0.5 cm of total length. While length classes of Table I are arranged according to this approximation, in the values of mean lengths allowance has been made for it by the addition of 0.5 cm to the figures calculated from the table. Age determinations are based on the study of scales. There is no information on details of technique. In his notes Dr. Lissner listed fishes of 1, 1+, 2, 2+, 3, 3+, etc., years of age. These determinations have been united for our purposes under the headings of 1, 2, 3 years, etc.

The two largest individuals observed were in the 20 cm class. The oldest individual observed was marked as 7 years old; it was in the highest length-class. The next lower age group of 6 years consisted of 16 fishes belonging to the 18 cm, 19 cm and 20 cm class.

For the reasons pointed out above, the 1-year group should be regarded with the utmost circumspection. Starting in the 5 cm class, it reaches up to 8 cm. No information is available on fish smaller than those of the 5 cm class. Of the total fishes studied the 1-year group comprises only 2.6%.

Table II presents the age groups and the respective average lengths. Growth curves plotted from these data are given in Figure 2. The first leg of the absolute growth curve (between 0 and 1) is purely hypothetical, as there are no basic data to support it. It has been assumed that the first-year ring is laid down during the first year after spawning. However, from the analysis of Dr. Lissner's data (see below) it will become clear that the year-of-life marks used by him are, in fact, laid down a few months after the completion of what is taken throughout this paper as the year of life. No correction with regard to this has been applied in the graphs.

TABLE II
Mean overall length of age groups (total 1218)

Age (years)	N	Mean overall length (cm)	Standard deviation	Standard error
1	32	7.19	1.1841	0.20958
2	187	9.97	1.0407	0.07610
3	393	12.07	0.9220	0.04651
4	445	14.02	0.8367	0.039664
5	144	16.46	1.2736	0.10613
6	16	(19.12)	(0.6000)	(0.1500)
7	1	(20.50)		

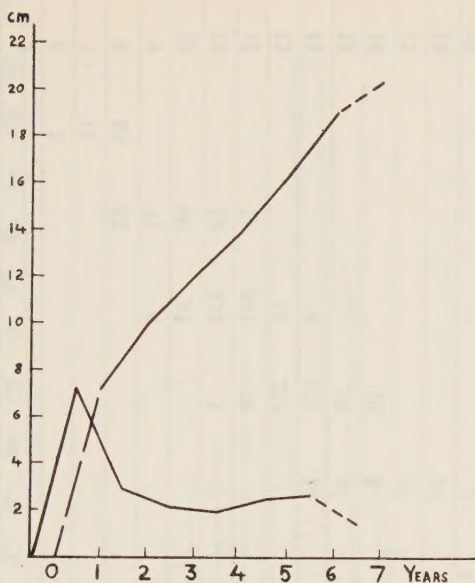


Figure 2

Absolute growth and annual increment

It is probable that the shape of the particular growth curves is not a true picture of the natural process in *Acanthobrama terrae-sanctae*. The essential weakness of the numerical raw material makes itself felt in the curves. This is more manifest in the curve of annual increments, where an upward inflection indicates the increment of the fourth year. Less reliable than any other part of the growth curves is the last leg, representing a single observation of the 7-year group.

Figure 3 illustrates the percentage representation of size classes in all samples. The rather abrupt drop in the representation rate of the large fishes is evident. Although this affects the 4-year group as well as the 5-year group (see Table III), the former group is still the largest of all (445 observations, see Figure 4). The 5-year group, comprising less than 12% of the total, constitutes a serious drawback for our computations. The still smaller sample in the 6-year group, with its 16 observations, is an additional factor of unreliability in the results obtained. Circumstances of this sort diminish the value of the growth curve.

In Table III the numerical relations between age groups and length classes are presented. The large middle groups, 3 and 4 years of age, will be considered first. Both of these extend over six length classes. The average total length of a fish of 3 years of age is 12.07 cm, but individually it varies from about 9.5 cm to about 14.5 cm or -21% and $+20\%$ of the mean total length. At 4 years the average fish is 14.02 cm long, the smallest about 11.5 cm, the largest about 16.5 cm; this means a variation of $\pm 18\%$ of the mean length. Including also the two adjoining age groups, we find that the overall variation of total length about the mean is 40% at

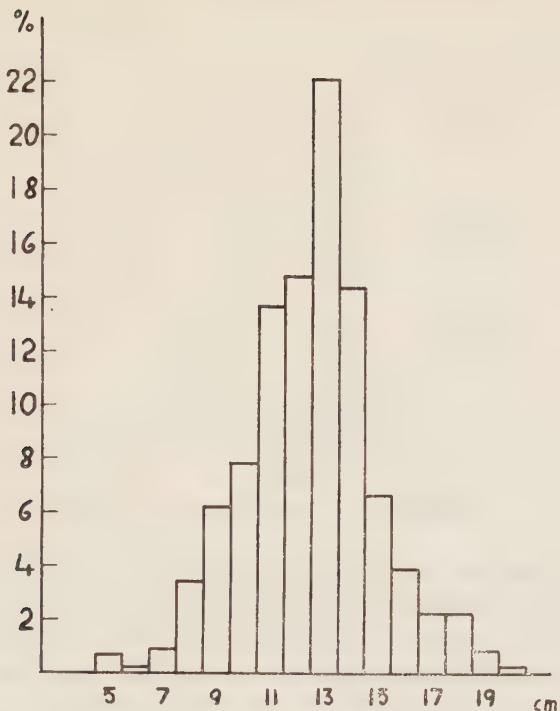


Figure 3
Distribution of length classes, all samples

2 years, 41.5 % at 3 years*, 35.6 % at 4 years, and 24.3 % at 5 years. There is a difference in the scatter of values insofar as in the 4-year group the 13 cm class is the largest one, including almost 50 % of the total; the lower classes comprise 6 %, the higher classes 44 %. In the 3-year group the 11 cm class is the largest one, comprising about 40 %, while the lower and the higher classes comprise 10 % and 50 % respectively. Concentration of values is, according to this, greater in the 4-year group. The 2-year and the 5-year groups have not been analysed from this point of view.

It is also important to appreciate the overlap of age groups. The table illustrates that the 2-year and the 3-year groups have four length classes in common, and the same relation exists between the 3-year and the 4-year groups. The 4-year and the 5-year groups, however, have not more than three length classes in common. A close study of the numbers reveals that it is the wide scatter of individuals of each group which—in terms of population—is exhibited as overlap of groups. Considering only the groups of 2, 3, 4, and 6 years, the smallest overlap is one of 45 % of the population in the 4-year group as related to the 5-year group. On the other hand, the overlap may amount to 90 % when the 3-year group is related to the 4-year group. A more detailed analysis of the significance of these relations would not be useful for obvious

* The significance of the difference between the age groups has not been calculated.

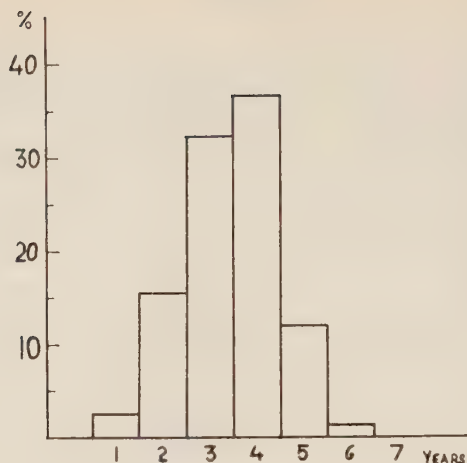


Figure 4

Representation of age groups, all samples

reasons. Yet, it should be noted that with regard to the extent of the length classes (read off in the horizontal direction, Table III) there is a common range of two classes for the 2-year and the 4-year groups, and of one class for the 3-year and the 5-year groups. Generally speaking, it appears that a spread over three age-groups is the normal condition of length classes in this species. This can be demonstrated by means of the 11 cm, the 12 cm, and the 14 cm classes, in which we find still another confirmation of the normalcy of this situation: the distribution pattern of the length class population, with a pronounced crowding in the median year group of every one of these length classes. These middle crowdings comprise 78.3% of the population in the 12 cm class, 86.4% in the 14 cm class, and as much as 91.6% in the 11 cm class. Small sections of the respective populations, 15.6% at the highest, belong to the younger or to the older group of the length classes. In other words, the 11 cm and the 12 cm classes are roughly 3 years old and the 14 cm class is roughly 4 years old. With reference to these deductions the condition of the 13 cm class presented in the same table does not appear normal. This is numerically the largest class, comprising 269 observations. Inserted between the classes just discussed, its population has a pronouncedly major part of individuals (80%) of 4 years of age and a minor part (20%) of those of 3 years of age. We have no explanation to offer for this exceptional situation.

An analysis of the length classes beyond those dealt with is not advisable with so narrow a material basis. For the same reason no comment is made concerning the length class composition of age groups. This is a serious deficiency since the wide scatter of the larger age groups (those represented by more than 100 individuals) would require further discussion. But whichever of the groups is singled out for analysis, its population reaches down into the lower length classes or up into the higher length classes which are themselves poorly represented and, as pointed out repeatedly, possibly ill-represented.

In spite of the small numbers involved, an attempt has been made to gain more insight into the seasonal life cycle of the population of *Acanthobrama terrae-sanctae*.

TABLE IV
Per cent incidence of total length classes in 2nd through 5th year group

2nd year						3rd year							4th year							5th year									
8	9	10	11	12	S	9	10	11	12	13	14	S	11	12	13	14	15	16	S	14	15	16	17	18	19	S	ΣS		
January					3	100					81			56					13					153					
March					18	50.6 44.5 4.9					18			58.9 37.5 3.6					14					20					70
April					46	27.8 55.6 16.7					26			28.6 42.8 14.3 14.3					88					12					172
May					32	38.5 19.2 38.5 3.9					53			67.0 31.8 1.1					30					4					119
June					40	3.7 9.4 37.7 32.7 17.0					43			3.4 6.7 46.7 33.4 6.7 3.4					1					5					89
July					31	46.5 46.5 7.0					51			100					40					21					143
Sept.						3.9 19.6 33.4 39.2 3.9					7			20.0 25.0 42.5 12.5					6					2					15
Oct.-Nov.					17	71.4 28.6					88			16.7 50.0 33.4					163					56					324
					187	38.6 44.3 17.0					367			15.3 47.2 31.9 4.3 1.2					398					133					1085

TABLE V
Age and total length of fish in monthly samples

L e n g t h c l a s s e s (cm)																	S																															
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20																																
When caught	Age (in years)																																															
	I	I	I	I	II	S ₈	II	III	S ₉	II	III	IV	S ₁₀	II	III	IV	S ₁₁	II	III	IV	S ₁₂	III	IV	V	S ₁₃	III	IV	V	S ₁₄	IV	V	S ₁₅	IV	V	S ₁₆	V	V	VI	S ₁₈	V	VI	S ₁₉	VI	VII	S ₂₀			
Oct. 1948										15		15		2	34		36		29		29		5	50	55		29	4	33		2	10	12		2	2	2	3								185		
Nov.																10	21	31		10	27	37		23	10	33		5	13	18		2	8	10	6		3	3		1	1					139		
Jan. 1949														3	41		44		36		36		4	33	37		21		21		2	6	8			4	4	3								153		
Sept.															5		5		2		1	3		3	3		2		2						2	2					1	1				16		
March 1950				1		1			1		1		3		3		3		11		5		16		10	4	14		3	6		9	2	4	6		2	1	3	4	11	2	13		1	1		74
Apr.																9	53	62		9	53	62		1	25	4	30			8		8													100			
May														1	9		11		9		2	11		11	11		1		1		1		1		1					1	1				44			
Feb. 1951							3		3		3	1	4		6		6		14		14		4	17	21		2	23		25		8		8		5	5	1	3		3	2		1	1	85		
Apr.		1	3	9	9	18			20		20		16	1	10		11		5		5		1	6	7		3		3		1		1													85		
May				2	2	10		2	12	13	4	17		11		11		8		8		9	3	12		9		9		1		1		1		1		1		2	1		1			76		
June	9	1	8		20	20		20		20		20	20		20		20		3		3		2	1	1											5	1	1	2	2	2	4		1	1		110	
July				1	1		17	2	19	10	10	20		3	17		20		20		20		2	8	10		10		10		17		17		5	13	18	6	2	2	2		3	3	1	1	2	148
Total	9	2	11	10	32	42	71	4	75	60	35	95	13	153	1	167	11	141	24	176	54	216	270	6	152	18	176	39	41	80	10	37	47	27	19	7	26	2	8	10	1	1	2		1215			

from the point of view of growth. In Table IV the length data of year groups are broken down according to months. The small 1-year and 6-year groups have been neglected. Basic counts per catch over different years, as shown in Table V, have been condensed and absolute values converted to percentage. In this arrangement one major trend stands out more or less clearly in each of the year groups: as the year progresses from the winter to spring and early summer months, the population of the lower length classes increases and/or more lower classes appear. This regression in average body length of the monthly population can have one explanation only. Individuals which have completed one annual cycle enter into the next higher one. This is done individually, as part of them rise at the same time into a higher length class, while others remain in their length class for an additional period (length classes have a range of 10 mm). Notwithstanding numerical limitations the significance of this shift is evident. It is brought out in identical fashion in several sections of the whole population studied. Because of the importance of this point we have selected for further analysis two parallel series (Table VI and Figure 5), the 3-year and the

TABLE VI

Monthly mean total length (cm) of 3rd and 4th year group, March through July

	3rd		4th	
	<i>m</i>	<i>n</i>	<i>m</i>	<i>n</i>
March	13.40	18	14.65	14
April	11.90	16	14.00	10
May	12.00	53	13.95	30
June	10.07	43	—	—
July	11.70	51	15.45	40

4-year groups. These groups are represented in all the catches to a greater extent than any other group. It can therefore be assumed that the material available for the months in question gives a fair picture of normal conditions. It is obvious from Table VI that although the data for the 3-year group are more complete and are based on larger numbers, there is a common tendency present in both groups: the decline of the mean length, starting in the month of March and reaching its lowest point in May or June, is followed by an increase in the mean length which becomes pronounced in July and, as is seen on further exploration of Dr. Lissner's data, goes on for the remainder of the annual cycle. Converted to diagrammatic form (Figure 5), the same basic data illustrate the accession to the year groups of length classes not represented in them before May (at least in the 3-year group). The fuller data of the 3-year group show that not only does a new class (11 cm) appear in the group as early as April, but that the maximum is shifted back from the 13 cm class to the new 11 cm class. Characteristically this is supplemented by the disappearance from the group of the highest length class, that of 14 cm length. The lability of the population, consequence of these age group shifts, is further demonstrated by the return in May

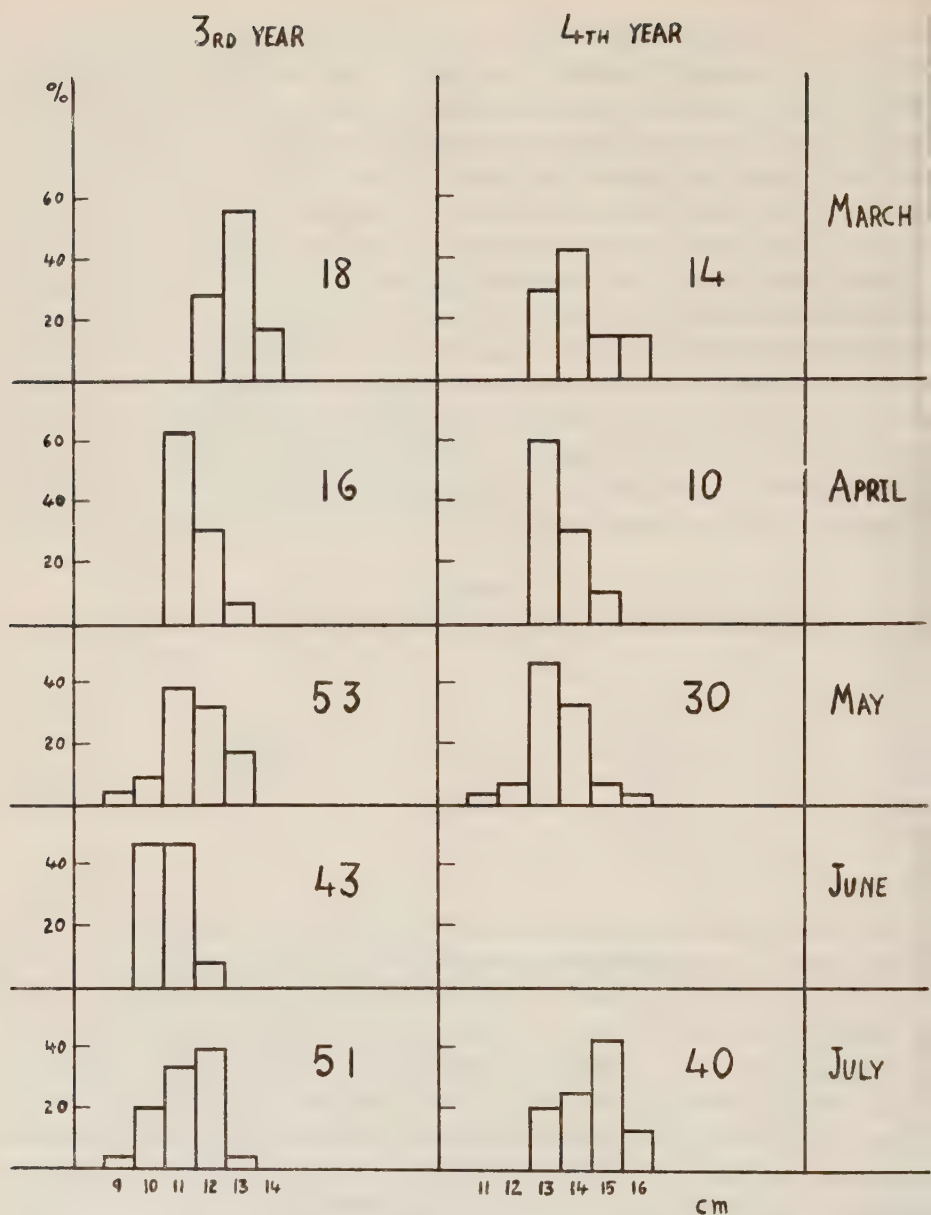


Figure 5
Incidence of length classes in 3rd and 4th year groups

of the maximum as it shifts forward to the 12 cm class, this move being supplemented by the numerical increase of the 13 cm class; at the same time two new classes (9 and 10 cm) enter the group. Fluctuations of this kind can, of course, be discovered in other groups too. The meaning of these fluctuations viewed as events affecting separate groups is a gain from the lower age group and loss to the higher one.

It must be kept in mind that the study of age groups and of shifts among them is based on the interpretation of scale readings. On the scale, the shift from one year group to the next expresses itself in structural details laid down between the months of March and June. Although this event is a more or less regular one in every year, it can by no means be assumed that the first event of this sort in the life of the fish necessarily coincides with the completion of its first year of life. As a matter of fact, the spawning season happens to fall in the period between December and March. The correspondence of the two 4-months periods, from December to March on the one hand and from March to July (Figure 5) on the other indicates that it takes about four months from the laying of the egg to the laying down of the scale focus.

PART 2. MERISTIC CHARACTERS

1. Fins

Substantial material had been collected by Dr. Lissner with the aim of establishing reliably the specific characters of *Acanthobrama terrae-sanctae*. The fins of more than 700 individuals were closely examined, furnishing a firm base for the average figures calculated by himself. The following tables are almost identical with those drawn up by Dr. Lissner.

TABLE VII
Frequency of counts in dorsal fin

Rays	10	11	12	13	S
<i>n</i>	4	747	8	1	760

$m = 11.01$

This fin count is remarkable for its consistency, as more than 98% of the 760 fish had 11 rays in the dorsal fin. The anal fin exhibits another point of interest (Table VIII), 89% of the fishes having either 16 or 17 rays in the anal fin.

TABLE VIII
Frequency of counts in anal fin

Rays	14	15	16	17	18	S
<i>n</i>	8	64	302	346	9	729

$m = 16.39$

Furthermore, the distribution of these most frequent values is not very far from even; 16 rays were observed in 46.5% and 17 rays in 53.5% of the 648 fishes concerned. It is not impossible that this distribution is the expression of a sex dimorphism in the species, which otherwise has so far been found only in

the difference of the length of the pelvic fins. As in many other species, the male has a considerably longer pelvic fin than the female (Steinitz 1952). The rays of both the pectoral and pelvic fins were counted on both sides of 729 individuals. Dr. Lissner was interested in judging the tendency for asymmetrical arrangement of fin rays.

TABLE IX
Frequency of counts in pectoral fin (both sides)

Rays	15/15	16/16	16/17	16/18	17/17	17/18	18/18	18/19	19/19
<i>n</i>	1	29	17	1	469	14	176	10	11

His table shows that 42 specimens out of 729 fall here (5.4%). It is obvious that 17 and 18 are the most frequent numbers of rays in this fin. The paired arrangement of counts fails, of course, to give an account of the frequency distribution of counts. If the 1458 counts actually performed are taken as the basis of computation, we find that the 17-ray count represents 66.5% of all cases, while the 18-ray count includes 25.9%. The general result of the study of the pelvic fin is very similar, if only the difference in absolute values is taken into account. It is noteworthy that again 42

TABLE X
Frequency of counts in pelvic fins (both sides).

Rays	8/8	8/9	9/9	9/10	S
<i>n</i>	13	36	674	6	729

individuals were observed to possess an asymmetrical arrangement of fin rays (5.4%). In the pectoral fin a variability of 25%, calculated from the maximum count of 20 rays, was found. The pelvic fin, with values much lower than those of the pectoral fin, has a variability of 20%. Also, whereas more than 92% of all cases are concentrated in the two most frequent counts of 17 and 18 for the pectoral fin, more than 95% of the pelvic fin counts are crowded into the 9-ray count. Summarising, it can be said that with regard to the fin counts there is remarkable uniformity of characters in *Acanthobrama terrae-sanctae*. It is perhaps worth adding that since nothing in the way of statistics has been published regarding other species of *Acanthobrama*, our statement does not prejudice any conclusions regarding the taxonomic interrelations of the members of the genus.

2. Vertebrae

Two hundred and three fish were dissected so as to lay bare the vertebral column. Staining with alizarin red S greatly facilitated the work. Dr. Lissner divided the vertebrae into pre-hemal and hemal ones and tabulated the results of his counts in the manner shown in Table XI. The total number of vertebrae ranged from 39 to 41, with the value of 40 including 154 specimens, or almost 76% of the total. About 16.5% of the fish had 39 vertebrae and about 7.5% had 41. Among those of the most frequent group, 84 (41.5%) had an

TABLE XI
Vertebral counts

	Pre hemal				
	19	20	21	22	
H 18	—	—	6	4	10
e 19	—	24	55	—	79
m 20	4	84	7	—	95
a 21	11	8	—	—	19
l	15	116	68	4	203

even subdivision of the vertebral column into 20 prehemal and 20 hemal vertebrae. A secondary high is pronounced where 55 fishes (35.5%) are found with 21 prehemal and 19 hemal vertebrae. A preference for 20 prehemal vertebrae on the one hand and 20 hemal vertebrae on the other may also be read off from the respective columns of Table XI, where we find a total of 116 fish (about 57%) with 20 prehemal vertebrae and of 95 fishes (47%) with 20 hemal ones. As there are no data available regarding the length of the fish examined, we have no way of knowing whether there is a shift of type of vertebrae during growth.

3. Gill rakers

Although Dr. Lissner had planned to include this character in his investigation, the counts of this kind were made after his death. The first branchial arch on both sides was subjected to this count in 97 fishes. The fish were also measured as to their body length (7–16 cm total length), but no correlation between the count and the size of the fish was discovered. Table XII shows the modal value to be 19 gill rakers,

TABLE XII
Frequency of gill raker counts

Gill rakers	16	17	18	19	20	21	S
<i>n</i>	1	1	11	46	34	4	97

the mean number being 19.27. The mode includes 47.5% of all individuals; the groups of 19 and 20 gill rakers together comprise 82.5% of the total.

PART 3. SEX AND MATURITY

What will be offered in this chapter is far from being conclusive. The material before us is broad and varified on the whole, but it should not be approached with the intention of drawing conclusions with regard to particular problems, for observational data are found insufficient in the numerical sense, or inconsistent as to sampling technique. Yet it would have been unjustifiable to neglect the enormous amount of work, the organised effort and the sum of data accumulated in the course of Dr. Lissner's study of the problems dealt with here. As we shall see, the scope of this study was wide from the outset, and the investigation ramified as it proceeded. But time ran out before an interim account to give definite direction and emphasis was prepared. Consequently we had to shape the data of Dr. Lissner into a first report. This has been done here; but it would have been unjust to leave it at

that. Dr. Lissner's preliminary results are thought-provoking, and if the present author accepts the responsibility for what may be judged a too speculative element of the opinions and suggestions advanced, it should not be overlooked that these are founded on the ample and sound work done by Dr. Lissner himself.

One of the lines of study followed by Dr. Lissner was the observation of the progress of the maturing gonads as related to the seasons of the year. He also compared the two sexes in order to find out whether both reached maturity at the same time. Whether he tried to find out if the various year (age) groups matured simultaneously or not is not quite certain, for the notes he left do not offer sufficient clues. On the other hand, numerous data were collected with respect to the sex ratio in the catches, yet again, in view of the small samples and the scanty notes accompanying the basic data, there is no point in drawing up a conclusive statement.

The following series of maturity stages was employed; part of them are easily applied to both sexes.

Stage I	Single eggs can not be discerned
II	Single eggs can be discerned
III	Eggs growing
IV	Eggs growing further
V	Eggs attain maximum size; ready to spawn
VI	After spawning

A female could be assigned to stage V without dissection if the slightest pressure on the abdomen produced fully developed eggs; in a male of this stage the pressure would produce a flow of sperm. If dissection of a male demonstrated flabby, narrow and more or less empty testes, it would belong to Stage VI. There are in Dr. Lissner's notes instances of males in Stages III and IV, but I am unable to present his definition for these. Nowhere was any mention made of males being in Stage I or II. It is fairly certain that Dr. Lissner never stated the sex of fishes without dissecting them, unless they were in Stage V.

1. Sex ratio

Sex diagnosis was made without the aid of a compound microscope. This was easy in large fishes and possible sometimes even in fishes of the 7 cm class (total length). Fishes only 6 cm long could not be sexed.

The analysis of dissections performed on fishes up to 8 cm had the interesting result that whenever the sex could be made out, it was male. Moreover, there is an obvious trend in the sex ratio of males being predominant in the smaller size classes, and the females constituting the majority of the catch in the larger classes. Equilibrium is maintained in the classes of 11 cm, 12 cm, or 13 cm, according to the sample. It is also seen that among the rare individuals of the classes larger than 15 cm there are almost no males at all. Taking for granted the general validity of these observations, they may be interpreted in this manner: while males become sexually mature at a smaller size than females, they do not grow to the same maximum size. The latter assumption is in line with the appearance of males in decreasing numbers towards the upper end of the size classes and their failure to appear in the top classes. The predominance of males among the smaller fish may be nothing but an expression of their maturation at an earlier growth-stage than that of the females. This suggestion is particularly fair if we assume, in addition, that schools* of *Acanthobrama terraesanctae* are composed of mature fish or of individuals approaching maturity, while specimens whose sex differentiation has not yet attained that degree have not

* Catches analysed for sexes were made during the reproduction period.

st joined the schools. If this proposition is thought too speculative in character, should at least stimulate reinvestigation of the questions discussed.

2. Growth of eggs

Significant information on the growth of the egg of the species is furnished by numerous counts and measurements. As far as I understand, several females were opened at one time, their ovaries excised and pooled, and random samples of eggs removed for measuring under the microscope, aided by a calibrated eyepiece micrometer. Sampling was done on three different occasions. The data obtained are condensed in Table XIII. Months are arranged so as to follow the progressing breeding season. This makes it clear that, as could be expected, eggs grow in conformity with the developing season. With the increase of mean size there is a distinct population

TABLE XIII
Average size of eggs during breeding season

Month	No. of females	No. of eggs	Mean	Diameter of egg (mm)		Mode
				Max.	Min.	
November	8	662	.699	1.045	.313	.770
February	2	267	1.015	1.510	.488	1.170
late March	3	97	1.462	1.900	1.100	1.400

shift, in the sense that at the beginning of the growth process the majority of the eggs have a diameter smaller than the modal value, and this is still the case in February; but at the end of the spawning period the majority of the eggs have a diameter greater than the modal value. This fits in well with the slow increase of the egg diameter, which after February becomes markedly steep. In other words, after a moderate onset of the breeding season, we observe something like an explosive development as the season draws towards its rather sudden end.

3. Fat reserves

In order to make his account of the maturation process as complete as possible, Dr. Lissner looked for cyclic changes in the intra-abdominal (intestinal) fat masses. He noticed that 227 fishes (9–17 cm, not sexed) dissected during October had considerable quantities of fat accumulated in the abdomen. One month later, marked masses of fat were again present, while the gonads were found “mostly in Stage III, narrow bands” (187 fishes). In January, 9 males and 7 females had “still some intestinal fat”; their gonads were in Stages III to IV/V. In February, in 21 individuals found to be in Stage IV or IV/V, no fat was noticed. In the latest check, made in early March on 140 fishes in Stage V or VI, none had noticeable fat.

The time of maximal fat accumulation cannot be fixed, since no observations are available covering the period from March till October. But it is evident, from what was observed so far, that the abdominal fat reserves are used up during the maturation of the gonads and at least until the release of the sex products.

4. Maturity in male and female

The January sample of 16 fishes mentioned above was also evaluated from another point of view. Apart from the sex diagnosis, a closer examination of the gonads was made and the details noted down (Table XIV). The point of major interest in the

TABLE XIV
Gonad stage in January sample: body size and sex

Length class (cm)	11	12	13	14	17
Number of specimens	1	3	9	2	1
Males: Number	1	3	5	—	—
Stage	III	III-IV; III-IV; III-IV	III; III; III-IV; III-IV; IV		
Females: Number	—	—	4	2	1
Stage			IV; IV-V; IV-V; IV-V	IV-V; IV-V	IV-V

table is the 13 cm class, the only one including both sexes. Among the males of this class, one individual reaches stage IV, the maximum stage for males in this sample; two males have as yet not passed stage III, the lowest stage for the length class. The females of the same length class start with stage IV, and three of them have already attained the maximal maturity of the whole sample. On the evidence of these figures one would be tempted to conclude that females mature prior to males in the same season. This does not invalidate the opinion expressed above that males differentiate sexually at a lesser body size than do females. Both statements require much more material before they can be settled conclusively.

5. Breeding season and spawning

Earlier in this paper we called the period from November to March the breeding season of *Acanthobrama terrae-sanctae*. The initial part of this period is indicated by certain behavioural traits, such as schooling and migration. They are observed at the time the sex cells start maturing and the intra-abdominal fat reserves start receding. Nowhere in Dr. Lissner's papers is there a note of the actual onset of spawning. However, all his relevant observations point to the later part of the breeding season.

6. Age of maturing fish

Another very important problem which has not been investigated in a direct manner is that of the age of fish passing through their first breeding season. We have only a few biostatistical data that have a bearing on this question. We have shown that the first year-class of fishes entering their 2nd year of life are, on the average, only little more than 7 cm long; they have grown up to about 10 cm when they finish it. They have reached 12 cm on the average when they complete their 3rd year of life. Linking these conclusions with the data treated in the present chapter, we should think that *Acanthobrama terrae-sanctae* probably starts breeding for the first time as it completes its 2nd year of life or enters its 3rd. However, there are numerous weak points in this deduction.

on, as we have repeatedly emphasised. Three major ones will be restated: no sex identifications are available of fishes whose age has been determined; the onset of actual spawning has not been fixed with sufficient precision; information concerning the maturation of the male is poor. I may add that Dr. Lissner's material does not exclude the possibility that part of the fish population enters the first breeding season at the beginning of the 2nd year of life, but likewise does not dismiss the possibility that a small part of the population is still not ready for spawning as it approaches the end of its 3rd year of life.

APPENDIX

The data collected by Dr. Lissner under the headings of Length frequency and Weight are not less extensive than those dealing with other aspects of the biostatistics of *Acanthobrama terrae-sanctae*. However, our information concerning the technique of catches and of sampling is almost nil. For this reason no comment will be made on the subject matter. The remarks added to the following tables are of purely technical nature.

1. Length frequency

A grand total of 2359 fish subjected to the analysis of incidence of total-length classes was collected in the course of 8 different months of the year. The months of April, June, August and December are not represented in this study. The fish conform to 14 length classes from 6 to 19 cm standard length. The lower length classes are missing in the catches of May, July and October.

In every month's catch the total number of fishes caught has been used for the calculation of per cent ratios of length classes which are shown in the main vertical columns of Table XV. The most frequent length class of the month stands out in bold type. On the table's right side the absolute size of monthly catches is given. Starting from the grand total of 2359, the per cent ratios of the various size classes in the whole catch were calculated. They are to be found in the last column.

2. Weight

The fish of the samples selected for weight determination were first measured and divided accordingly into length classes. The lots of the various length classes were then weighed separately to the nearest gram. In Table XVI the cumulative weight of these single lots is not included. The mean weight is given to the tenth of a gram.

There are no samples available for the months of January, August, November and December. Five months of the year are represented by one sample and only three months by two samples. Of all the samples, only four make up one continuous seasonal group (April through July, 1951); yet two of the samples are very small. Although there are numerous reliable single data concerning body weight, the shortcomings of the material as a whole did not justify the elaboration of monthly

TABLE XV
Per cent ratio of length frequency in monthly and in total catch

Total length (cm)	Per cent ratio in monthly catch												Monthly catch N	Monthly catch %
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII		
6	.9	2.2	.6	—	—	—	—	—	8.2	—	.7	—	43	1.8
7	.4	1.5	1.3	—	—	—	—	—	7.3	—	2.1	—	43	1.8
8	.4	.7	2.3	1.7	—	—	—	—	1.9	—	2.7	—	36	1.5
9	.9	7.4	2.6	14.5	1.8	—	—	—	13.6	1.8	.3	—	176	7.5
10	3.8	5.2	5.5	33.9	4.6	—	—	—	27.9	8.8	1.0	—	393	16.7
11	21.1	8.9	19.4	20.9	3.7	—	—	—	22.5	21.6	4.1	—	412	17.5
12	22.8	18.5	26.9	11.6	14.7	—	—	—	9.0	34.8	19.6	—	425	18.0
13	25.5	23.7	23.3	8.3	22.0	—	—	—	6.8	23.8	24.1	—	393	16.7
14	12.3	15.6	9.7	3.3	25.7	—	—	—	1.2	6.8	13.7	—	218	9.3
15	6.4	9.6	6.2	1.3	18.4	—	—	—	.7	.4	12.7	—	116	4.2
16	3.4	4.4	1.9	1.3	6.4	—	—	—	.2	.9	4.5	—	51	2.2
17	2.6	2.2	—	2.8	1.8	—	—	—	.2	1.3	2.4	—	40	1.7
18	—	—	.3	.3	.9	—	—	—	.2	—	1.7	—	10	0.4
19	—	—	—	.2	—	—	—	—	.2	—	.3	—	3	0.1
Total monthly catch	235	135	309	—	640	—	109	—	413	227	291	—	2359	

Mean weight of length classes in monthly samples (total: 2510)

		Total length in cm																
		5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	SN	
Oct. 1948	n					4	20	49	10	54	15	1	2	3			227	
	m. w.					7.5	7.5	11.8	15.0	19.2	23.3	30.0	35.0	48.3				
Feb. 1949	n	3	2	1	10	7	10	20	27	15	12	4	3				114	
	m. w.	3.0	4.5	8.0	10.0	6.5	10.0	12.0	15.8	19.6	24.7	32.5	37.5	46.7				
March 1949	n	2	4	7	8	17	60	83	72	30	19	6			1		309	
	m. w.	5.0	4.0	5.6	7.0	9.7	12.0	15.7	20.0	24.3	29.2	36.7			60.0			
May 1949	n			11	85	165	98	47	22	4	4	8	17	2	1		464	
	m. w.			5.5	7.2	9.2	11.7	17.0	20.9	28.8	36.5	46.3	48.8	55.0	75.0			
July 1949	n				2	5	4	16	24	28	20	7	2	1			109	
	m. w.				5.0	8.0	11.3	16.9	20.4	25.7	32.0	40.0	45.0	60.0				
Sept. 1949	n	34	30	8	56	115	93	37	28	5	3	1	1	1	1		413	
	m. w.	2.2	2.8	5.0	6.7	8.3	11.5	15.4	18.0	24.0	36.7	45.0	50.0	65.0	70.0			
Feb. 1951	n						6	14	21	25	8	5	1	3	2		85	
	m. w.						12.0	15.9	20.1	24.8	31.3	36.4	42.0	57.3	61.0			
Apr. 1951	n	1	3	18	20	16	11	5	7	3	1						85	
	m. w.	2.0	3.3	4.7	6.0	7.8	10.2	13.0	15.7	26.6	30.0							
May 1951	n			2	12	17	11		12	9	1	1	2	1			68	
	m. w.			7.5	7.9	13.8	15.5		21.7	25.0	30.0	35.0	47.5	50.0				
June 1951	n	9	8	28	126	146	35	3	1			1	2	4	1		364	
	m. w.	1.1	2.5	5.0	6.5	8.5	11.1	13.3	20.0			50.0	45.0	52.5	70.0			
July 1951	n			2	16	47	93	51	10	10	17	18	6	1	1		272	
	m. w.			6.0	6.9	9.2	11.8	15.7	21.2	26.0	33.5	38.3	44.2	50.0	60.0			
	N	9	40	47	77	339	555	470	355	278	144	86	53	37	14	6	2510	
	W	10	96	140	399	2290	5020	5451	5562	5489	3590	2750	2092	1747	777	397	35810	
	M. W.	1.1	2.4	3.0	5.2	6.8	9.0	11.6	15.7	19.7	24.9	32.0	39.4	47.2	55.5	66.2	14.3	
	n	n number of fish	m. w., M. W. mean weight of fish															n

or seasonal fluctuations of the weight of *Acanthobrama terrae-sanctae*. On the other hand, the grand total of individuals as well as the totals of the length classes constitute a fair basis for the calculation of mean weights once the monthly samples are pooled together. Plotted against the standard length (Figure 6), they illustrate the increase of weight during growth from 5 cm to 19 cm.

ACKNOWLEDGEMENTS

Throughout the study of *Acanthobrama terrae-sanctae* Dr. Lissner was assisted by Mrs. E. Krause. Mrs. Krause continued to extend her valuable help to the present writer during the initial phase of his work on Dr. Lissner's material. Discussions with Dr. Lissner's co-workers in the Sea Fisheries Research Station contributed

greatly towards the conclusions arrived at. Without the participation of Mrs. H. Hornung of the Sea Fisheries Research Station in the statistical treatment of the majority of the samples, the publication of Dr. Lissner's observations would have been impossible. Miss H. Stettiner checked a great many of my calculations, compiled numerous tables and helped draw the graphs.

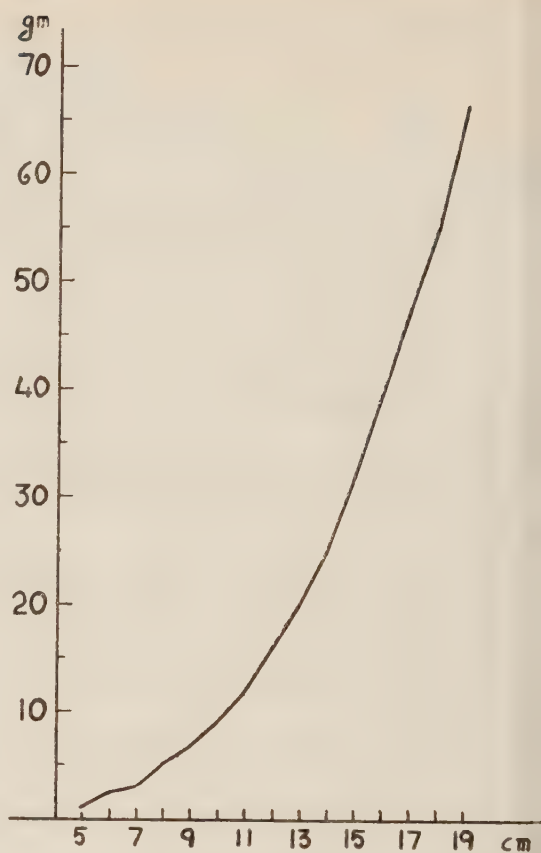


Figure 6
Weight and length

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THE PLANKTON OF LAKE TIBERIAS

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ABSTRACT

This study is based on a collection of monthly plankton samples taken over a period of two years at a number of stations on Lake Tiberias, at depths ranging from 10 m to 30 m.

The plankton volumes obtained by vertical haulings suggest the existence of two major seasonal pulses, one during the winter and a second during the summer months; a third, minor pulse occurs in spring, due to a heavy periodic water-bloom caused by *Peridinium westi*.

A systematic account of the main phytoplankton and zooplankton components is given. The phytoplankton was found to consist of numerous species, among which the Chlorophyceae dominate over the Cyanophyceae. A special study was made of the seasonal and local variations in body shape of *Ceratium hirundinella*. Of the local variations in the populations of this phytoflagellate, some correspond to well-defined types, while others seem to be specifically characteristic of Lake Tiberias due to its geographical isolation as a fresh-water habitat. The zooplankton, which is better known from previous investigations, appears to have remained unchanged both in composition and relative abundance throughout the years. It consists of a relatively small number of species belonging mainly to rotifers, cladocerans and copepods. Among the latter a marked absence of diaptomids was observed.

A study of the vertical distribution of plankton organisms during the stagnation period in May-June showed a fairly uniform distribution within the epilimnion down to the thermocline. No zooplankton representatives whatsoever were found in the oxygen-deficient hypolimnion, while the microscopic algae were limited to a few species occurring in low numbers.

The classification of Lake Tiberias in the light of accepted systems based on productivity is discussed. Due to mixed eutrophic, oligotrophic and even dystrophic characteristics, the lake could not be defined within the terms of such a framework. It is suggested that tropical and subtropical lakes rather than temperate ones be used when discussing the classification of Lake Tiberias.

An outline of future work based on the data obtained from the present investigation is proposed.

INTRODUCTION

During the latter part of 1948 the Sea Fisheries Research Station undertook an investigation of the hydrographical and biological conditions prevailing in Lake Tiberias. This work, which was continued through 1949 and 1950, was initiated by Dr. H. Lissner, the late Director of the Station. He entrusted the author with the examination of the plankton samples that he himself had collected during a period of one year, from November 1948 to October 1949, this material forming the basis of this report. The author continued sampling plankton at the lake for another year at the same stations and by the same methods used by Dr. Lissner.

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During May and June, 1950, the author had the opportunity of examining the plankton obtained by the sedimentation method from water samples collected by O. H. Oren*, the hydrographer of the Station. These samples were collected over a number of stations at various depths (Figure 1) and provided the material for preliminary examination of the vertical distribution of the main plankton components.

MATERIAL AND METHODS

The material was collected at monthly intervals along two profiles drawn from Tiberias to Ein Gev and Ginossar to El Kursi. Vertical samples were taken at depths of 10, 20 and 30 metres by hauling a plankton net made of No. 18 bolting silk from each of these depths to the surface. The specifications for the net were: internal diameter of the mouth — 26 cm; length of cylindrical canvas sleeve — 17 cm; length of conical silk portion — 55 cm. The bucket was of a cylinder-shaped type, 5.25 cm in diameter and 8 cm in length. The bottom was covered with bolting silk of the same mesh as the conical silk portion.

Owing to the comparatively large size of the meshes, it was obvious that a considerable proportion of the smaller organisms was lost during the hauling of the net, including most of the nanoplankton such as flagellates, the smaller protozoa and unicellular algae. The samples, therefore, were chiefly representative of the macroplankton and microplankton of the lake, such as planktonic Entomostraca, Rotifera, aquatic insect larvae and the larger Ciliata of the zooplankton, as well as dinoflagellates, the larger diatoms and other unicellular algae occurring in larger concentrations of the phytoplankton. Since the organisms belonging to the above groups constituted by far the main components of the plankton population, their identification was carried out, in most cases, to the level of species or even varieties. Observations were made on the main seasonal fluctuations of the individual species with a view to correlating them with the monthly diet of the plankton-feeding fish.

In the course of an investigation carried out on the food of *Acanthobrama terraesanctae* (Komarovsky 1952) and of the cichlid fishes of Lake Tiberias (Ben-Tuvia 1953), the author had the opportunity of recording additional species of plankton organisms which were not encountered in the net plankton owing to their small size.

The sedimentation method for plankton examination was used in the case of the samples collected by O.H. Oren and associates (May and June 1950). Concentrated formalin was added to volumes of 100 cc of lake water from various depths to obtain a concentration of 4%.

REVIEW OF LITERATURE

Most papers on the plankton of Lake Tiberias deal chiefly with the fauna rather than the flora of the lake. Various authors have contributed in this field by occasional

* In collaboration with the Departments of Irrigation and Hydrology of the Ministry of Agriculture and the Research Council of Israel.

CONTOUR MAP OF LAKE BOTTOM



reports on individual zooplankton groups (Tristram 1888, Richard 1893, 1899, Gurney 1913, 1933, Rousselet 1913). It is, however, mainly due to the investigations of Barrois (1894) and Annendale (1916) that we today possess a more or less general survey of the zooplankton of Lake Tiberias. These two investigators, however, visited the lake at different times of the year, the former in May, following the end of the rainy season, when the level of the water was at its highest, and the latter in October, just before the beginning of the rains, when the level of the water was at its lowest. It is therefore not surprising that Barrois and Annendale offered rather contradictory evidence concerning the vertical stratification of some of the important plankton organisms recorded in the lake. Barrois, for instance, mentioned, in his report, finding plankton organisms at all depths down to over 40 m, whereas Annendale found such organisms down to a depth of only 22 m, this apparently being due to the different circulation periods in the lake at the time of sampling plankton (Oren 1952, 1957). The main zooplankton groups of Lake Tiberias are also included in Bodenheimer's (1935) survey of the fauna of the lake.

While the zooplankton of the lake is thus comparatively well known, very little work has been done on the phytoplankton. Barrois (1894) made an incidental reference to the green algae constituents of the lake plankton by pointing out that their high concentration was one of the reasons for the low transparency of the lake water (3–4 m as compared to 9–10 m in the Swiss lakes).

Hornell (1934), in a report on the fisheries of Palestine, mentions the influence of the inflow of waters rich in nutrients from Lake Huleh and adjoining wadis on the productivity of Lake Tiberias. According to this author, the inflow which takes place during the rainy season from January to April is responsible for the phytoplankton pulse taking place at this time of the year, which in turn provides food for the "incredibly numerous swarms of copepods and cladocerans."

Rayss (1944), in her report on the Cyanophyceae of Palestine, in which she lists 60 species of algae belonging to this group which she recorded from various parts of the country, mentions 4 species of Chroococcales as occurring in Lake Tiberias. Two of these, *Microcystis flos aquae* and *M. aeruginosa*, have been observed by Rayss to cause frequent water-blooms. In a second report on the fresh-water algae of Palestine, the same author (1952) adds another 26 species found by her in the plankton of Lake Tiberias which belong to the following systematic groups, given in the same order in which they are listed: Peridineae (3), Heterokontae (1), Diatomeae (3), Chlorophyceae (17) and Desmidiaceae (2). Further references concerning individual species recorded by Rayss in the plankton of Lake Tiberias will be made in the course of this report.

The present author has cited the case of two plankton algae, *Fragillaria crotonensis* Kitton and *Peridinium westi* Lemm., as causing conspicuous blooms in the lake at certain times of the year (Komarovsky 1951). The author also gave a list of common phytoplankton and zooplankton organisms in his report on the food of *Acanthobrama terra-sanctae*, the well-known "Tiberias sardine" from Lake Tiberias (Komarovsky 1952), economically one of the most important fish species in the lake.

SEASONAL FLUCTUATIONS OF THE PLANKTON

In order to obtain a general idea of the fluctuations in plankton abundance throughout the year, the monthly samples from both profiles were subjected in the laboratory to the sedimentation method in conical graduated tubes. As the samples were always taken at the same stations along the set profiles and roughly at the same morning hours, the monthly plankton volumes from various depths (10, 20, 30 m) could provide a basis of comparison. These values were considered separately for each depth, and mean values were also computed for the six stations examined in any one month in order to avoid putting too much stress on fluctuations of a local character.

TABLE I*

Data on the quantity of plankton recorded by the sedimentation method (in cc) at Tiberias and Ginossar, November 1948–September 1949

Month	10–0 m	Tiberias 20–0 m	30–0 m	10–0 m	Ginossar 20–0 m	30–0 m
Nov.	0.22	0.20	0.33	—	—	0.20
Dec.	0.30	0.35	0.35	0.50	0.40	0.50
Jan.	1.15	0.50	0.70	—	—	—
Feb.	1.65	1.25	1.10	0.55	1.10	1.60
March	0.40	0.65	—	0.50	1.20	0.55
April	0.45	1.00	0.75	0.35	0.90	0.70
May	1.50	1.65	0.60	1.00	0.90	1.30
June	0.90	0.95	0.45	0.55	0.43	—
July	0.65	1.70	0.50	4.00	1.70	2.80
August	0.80	2.10	2.80	—	3.30	2.50
Sept.	1.90	3.00	1.50	0.80	2.20	3.20

* The numbers represent the volumes of plankton in cc collected by hauling the net through water columns of 10, 20, and 30 m. Where no number is given, no material was collected for technical reasons.

The values appearing in Table I suggest the existence of two annual maxima in plankton production, one in January and February, which subsided in March, and a second, rather more pronounced one during July, August and September. While the winter maximum is caused mainly by diatom and peridinin blooms, the summer maximum is caused by a variety of groups, among which Entomostraca and some blue-green algae are the main components.

Our data also tend to indicate a slight secondary pulse during April and May which coincides with the heaviest peridinin blooms occurring in the lake (Komarovskiy 1951).

The occurrence of the winter and summer maxima in Lake Tiberias as distinct from the spring and autumn ones which generally occur in natural bodies of water is similar to that encountered by the author while studying the plankton of fish ponds

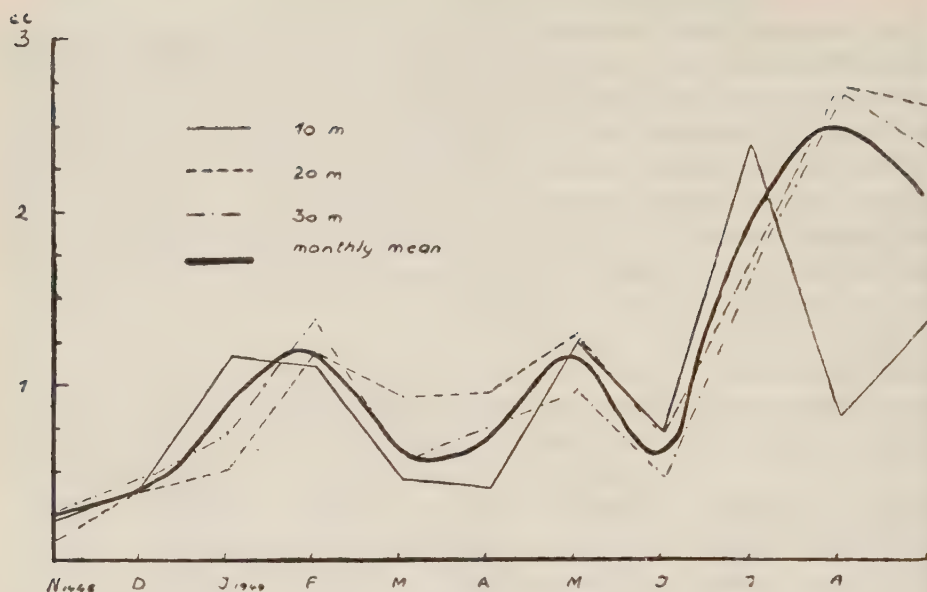


Figure 2

Seasonal fluctuations of the plankton in Lake Tiberias at various depths (based on samples collected off Tiberias and Ginossar)

in the Beisan Valley, which like Lake Tiberias are also situated below sea level (Komarovsky 1953). It is therefore suggested that these unusual pulses in plankton abundance in the water bodies of the Jordan Rift Valley may be connected with the geographical and topographical nature of the region.

These peaks in plankton abundance in Lake Tiberias coincide with the highest catches of *Acanthobrama terraе-sanctae*, as successive annual reports of the Fisheries Department indicate.

A similar correlation was found to exist between the spring and late autumn plankton pulses off the Mediterranean Coast of Israel and the catches of *Sardinella aurita* (Komarovsky 1956, Ben-Tuvia 1956).

There are, however, a number of discrepancies in the values of plankton volumes at certain depths, such as the volume of a vertical sample at 30 m sometime being lower than at 10 m or 20 m in spite of the higher water column filtered by the net. Such cases, although not improbably due to shore influences and other factors, such as the irregular and non-homogeneous horizontal distribution of the plankton (Worthington and Ricardo 1936, Botnariuc 1954), require further elucidation over a number of years, carried out at a large number of points over the lake by the best available methods for quantitative estimations.

SYSTEMATIC LIST OF PLANKTON ORGANISMS

A. THE PHYTOPLANKTON

CYANOPHYCEAE

CHROOCOCCALES

Family CHROOCOCCACEAE

- | | |
|---|--|
| <i>Aphanocapsa pulchra</i> (Kütz.) Rabenh. | <i>Holopedia dieteli</i> (Richter) Migula |
| <i>Aphanocapsa endophytica</i> G. M. Smith | <i>Merismopedia glauca</i> (Ehrbg.) Naegeli |
| <i>Aphanothece nidulans</i> Richter | <i>Merismopedia minima</i> Beck |
| <i>Chroococcus limneticus</i> Lemmerm. | <i>Microcystis aeruginosa</i> (Kütz.) Elenk. |
| <i>Chroococcus minutus</i> (Kütz.) Naegeli | <i>Microcystis firma</i> (Bréb. and Lenorm.) Rabenh. |
| <i>Chroococcus turgidus</i> (Kütz.) Naegeli | <i>Microcystis flos aquae</i> (Wittr.) Kirchn. |
| <i>Coelosphaerium dubium</i> Grunow | <i>Microcystis ichthyoblabe</i> Kütz. |

HORMOGONALES

Family OSCILLATORIACEAE

- | | |
|---|--|
| <i>Lyngbia cryptovaginata</i> Schkorbatow | <i>Oscillatoria</i> sp. |
| <i>Lyngbia limnetica</i> Lemmerm. | <i>Spirulina platensis</i> (Nordst.) Geitler |
| <i>Oscillatoria constricta</i> (Szafer) Geitler | |

Family NOSTOCACEAE

- Anabaenopsis circularis* (G. S. West) V. Miller

DIATOMAEAE

Family COSCINODISACEAE

- | | |
|--|---|
| <i>Cyclotella catenata</i> Brun. | <i>Melosira granulata</i> v. <i>angustissima</i> Müller |
| <i>Melosira granulata</i> (Ehrbg.) Ralfs | |

Family FRAGILARIACEAE

- | | |
|--|--------------------------------------|
| <i>Fragilaria crotonensis</i> Kitton | <i>Synedra ulna</i> (Nitzsch) Ehrbg. |
| <i>Synedra affinis</i> Kütz. v. <i>fasciculata</i> (Kütz.) Grunow* | |

Family ACHNANTHACEAE

Cocconeis sp.

Family NAVICULACEAE

- | | |
|---|---|
| <i>Amphora ovalis</i> Kütz.* | <i>Gyrosigma acuminatum</i> (Kütz.) Rabenh. |
| <i>Cymbella affinis</i> Kütz. | <i>Navicula</i> sp. |
| <i>Cymbella cymbiformis</i> (Ag.) Kütz. | <i>Stauroneis anceps</i> Ehrbg. |
| <i>Gomphonema</i> sp. | |

Family SURIRELLACEAE

- | | |
|--|---------------------------------|
| <i>Cymatopleura solea</i> (Bréb.) W. Smith | <i>Surirella robusta</i> Ehrbg. |
| <i>Surirella ovalis</i> Bréb. | |

CHLOROPHYCEAE

PROTOCOCCALES

Family CHARACIACEAE

- | | |
|---|---|
| <i>Characium debaryanum</i> (Reinsch) De Toni | <i>Characium hookeri</i> (Reinsch) Hansg. |
|---|---|

* Found in food of cichlid fishes

Family HYDRODICTYACEAE

- | | |
|---|---|
| <i>Pediastrum boryanum</i> (Turpin) Menegh. | <i>Pediastrum duplex</i> v. <i>coronatum</i> Racib. |
| <i>Pediastrum simplex</i> (Meyen) Lemm. | <i>Pediastrum ovatum</i> (Ehrbg.) A. Braun |
| <i>Pediastrum duplex</i> Meyen f. t. | <i>Pediastrum tetras</i> (Ehrbg.) Ralfs* |
| <i>Pediastrum duplex</i> v. <i>clathratum</i> (A. Br.) Lag. | |

Family OÖCYSTACEAE

- | | |
|--|---|
| <i>Ankistrodesmus falcatus</i> (Corda) Ralfs f. t. | <i>Lagerheimia longiseta</i> Lemmerm. |
| <i>Ankistrodesmus falcatus</i> v. <i>duplex</i> (Kg.) G. S. West | <i>Oöcystis solitaria</i> Witr. |
| <i>Ankistrodesmus longissimus</i> (Lemmerm.) Wille | <i>Oöcystis</i> sp. |
| <i>Kirchneriella lunaris</i> (Kirchner) Moebius | <i>Tetraëdron muticum</i> (A. Br.) Hansg. |

Family DICTYOSPHAERIACEAE

- | | |
|---|--|
| <i>Dictyosphaerium ehrenbergianum</i> Naegeli | <i>Dictyosphaerium pulchellum</i> Wood |
|---|--|

Family SCENEDESMACEAE

- | | |
|---|--|
| <i>Crucigenia tetrapedia</i> (Kirchn.) W. and G. S. West | <i>Scenedesmus bijugatus</i> β . <i>alternans</i> (Reinsch) Hansg. |
| <i>Scenedesmus acuminatus</i> (Lagerh.) Chod. | <i>Scenedesmus obliquus</i> (Turp.) Kg. |
| <i>Scenedesmus bijugatus</i> α . <i>seriatus</i> Chod. | <i>Scenedesmus quadricauda</i> (Turp.) Bréb. |

Family COELASTRACEAE

- | | |
|---------------------------------------|---|
| <i>Coelastrum microporum</i> Naegeli | <i>Coelastrum reticulatum</i> (Dangeard) Senn |
| <i>Coelastrum proboscideum</i> Bohlin | |

Family MICRACTINIACEAE

- Golenkinia radiata* Chod.

VOLVOCALAE

Family VOLVOCACEAE

- Eudorina elegans* Ehrbg.

TETRASPORALAE

Family PALMELLACEAE

- | | |
|---|---------------------------------------|
| <i>Gloeocystis botryoides</i> (Kütz.) Naegeli | <i>Sphaerocystis schroeteri</i> Chod. |
|---|---------------------------------------|

ULOTRICHALAE

Family MICROSPORACEAE

- Microspora stagnorum* (Kütz.) Lag.

HETEROKONTAE

Family CHLOROBOTRYDACEAE

- Chlorobotrys regularis* Bohlin

Family BOTRYOCOCCACEAE

- Botryococcus braunii* Kütz.

CONJUGATAE

Family DESMIDIACEAE

- | | |
|---------------------------------------|----------------------------------|
| <i>Spondylosium moniliforme</i> Lund* | <i>Staurastrum muticum</i> Bréb. |
| <i>Staurastrum gracile</i> Ralfs | |

* Found in food of cichlid and other fishes.

PERIDINEAE

Family KYRTODINIACEAE

Glenodinium cinctum Ehrbg.

Family KROSSODINIACEAE

Ceratium hirundinella O. F. Müller*Peridinium bipes* Stein*Diplopsalis acuta* (Apstein) Entz-fil.*Peridinium westi* Lemmerm.*Gonyaulax apiculata* (Penard) Entz-fil.

EUGLENINAE

Family EUGLENACEAE

Euglena acus Ehrbg.

CRYPTOMONADINAE

Family CRYPTOMONADACEAE

Cryptomonas erosa Stein

B. THE ZOOPLANKTON

SARCODINA

Order Aphrothoracida

Actinophrys sp.

CILIATA

Order OLIGOTRICHIA

Halteria sp.

Order PERITRICHIA

Vorticella sp.*

NEMATHELMINTES

Free living nematodes

ROTATORIA

Family SYNCHAETIDAE

Polyarthra remata Skorikov*Synchaeta pectinata* Ehrbg.*Polyarthra vulgaris* Carlin

Family ANURAEIDAE

Anuraeopsis fissa (Gosse)*Keratella valga tropica* (Apstein)*Keratella cochlearis* (Gosse)

Family BRACHIONIDAE

Brachionus budapestensis Daday

Family ASPLANCHNIDAE

Asplanchna brightwellii Gosse*Ascomorpha saltans* Bartsch

Family PEDALIONIDAE

Pedalia fennica (Lavander)*Pedalia intermedia* Wiszniewski*Pedalia fennica oxyure* (Zernov)*Triarthra longiseta* Ehrbg.

UNCLASSIFIED

Ephiphanes sp.*Platyas patulus* (Ehrbg).

* Probably found accidentally in the plankton.

CRUSTACEA

CLADOCERA

Family BOSMINIDAE

Bosmina longirostris (O. F. Müller) *Bosmina longirostris* var. *cornuta* Jurine

Family SIDIDAE

Diaphanosoma brachyurum (Liéven)

Family DAPHNIIDAE

Ceriodaphnia reticulata (Jurine)

Daphnia lumholtzi Sars

Ceriodaphnia rigaudi Richard

Family CHYDORIDAE

Alona affinis Leydig*

Chydorus sphaericus (O. F. Müller)*

COPEPODA

Family CYCLOPIDAE

Mesocyclops leuckarti Claus

Thermocyclops dybowskii Lande

OSTRACODA

Family CYTHERIDAE

Limnocythere tiberiadis Moniez

GENERAL DISTRIBUTION

The data presented in this chapter regarding the occurrence of various organisms in the plankton at different times of the year relate only to the "net plankton" and do not include such organisms as have been occasionally encountered in the examination of the food of pelagic fish.

On the whole, no basic differences in composition at any time of the year have been observed between the plankton samples collected off Tiberias and those collected off Ginossar. This shows that a fairly uniform distribution of the plankton in Lake Tiberias is to be expected, although some changes of a local nature may be induced by the River Jordan along its course, as well as by brackish and thermal water sources, as suggested by Barrois (1894).

The seasonal fluctuations both in the composition and in the quantity of the plankton due to the swarming or blooming of various organisms at certain times of the year similarly seem to affect the lake as a whole. The stability of the biocenose existing in the lake, at least as far as plankton is concerned, will be considered later in this paper in the light of observations carried out by previous investigators and by ourselves.

NOTES ON THE MAIN CONSTITUENT PLANKTON GROUPS AND ORGANISMS

The phytoplankton

CYANOPHYCEAE

The Cyanophyceae, although present in most of the plankton hauls, never form actual blooms of the type customarily encountered in fish ponds of this region (Komarovskiy 1951, 1953).

* Found in food of *Acanthobrama terrae-sanctae*.

TABLE II

Monthly occurrence of main groups of plankton organisms in Lake Tiberias, November 1948–October 1949, at Tiberias (T) and Ginosar (G)

	XI		XII		I		II		III		IV		V		VI		VII		VIII		IX		X	
	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G
HYTOPLANKTON																								
CYANOPHYCEAE																								
<i>Nabaenopsis circularis</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	—
<i>Phanocapsa pulchra</i>	+	+	+	+	+	0	—	—	—	—	—	—	—	—	+	+	+	+	—	—	+	+	+	+
<i>Phanocapsa endophytica</i>	+	+	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+
<i>Phanotheece nidulans</i>	+	+	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+
<i>Micrococcus minutus</i>	—	—	+	+	—	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Micrococcus limneticus</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Micrococcus turgidus</i>	—	—	—	—	—	0	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Coelosphaerium dubium</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	—
<i>Volvox dietlei</i>	—	—	—	—	+	0	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Synechococcus cryptovaginata</i>	+	+	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+
<i>Synechococcus limnetica</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+
<i>Microcystis flos-aquae</i>	+	+	+	+	+	0	+	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Microcystis aeruginosa</i>	+	+	—	—	+	0	—	—	—	—	—	—	+	+	—	—	—	—	+	+	+	+	—	—
<i>Microcystis ichtyobolae</i>	+	+	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	—
<i>Microcystis firma</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	—
<i>Scillatoria</i> sp.	—	—	—	—	+	0	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—
<i>Pirulina platensis</i>	—	—	—	+	—	0	—	—	—	—	+	—	+	+	—	—	—	—	—	—	—	—	—	—
DIATOMEAE																								
<i>Gyrodinium affinis</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
<i>Gyrodinium solea</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	+	+	—	—	+	—	—	—
<i>Homphonema</i> sp.	—	—	—	—	—	0	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Gyrodinium acuminatum</i>	—	—	+	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Frustularia crotonensis</i>	—	—	—	—	+	0	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aelosira granulata</i>	+	+	+	+	+	0	+	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Navicula</i> sp.	—	—	—	—	—	0	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Surirella ovalis</i>	—	—	—	—	—	0	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Surirella robusta</i>	—	—	—	—	—	0	—	—	—	—	—	—	+	+	—	—	—	—	—	—	+	—	—	—
<i>Stauroneis anceps</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Synedra ulna</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
CHLOROPHYCEAE																								
<i>Ankistrodesmus longissimus</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ankistrodesmus falcatus</i>	—	—	—	—	—	0	—	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Characium debaryanum</i>	+	+	—	—	+	0	—	—	—	—	+	—	—	—	+	+	—	—	+	+	+	+	—	—
<i>Coelastrum reticulatum</i>	—	—	—	—	—	0	—	—	—	—	—	+	—	—	+	+	—	—	—	—	—	—	—	—
<i>Coelastrum microporum</i>	—	—	—	—	+	0	—	—	+	+	+	+	+	+	—	—	—	—	—	—	—	—	—	—
<i>Crucigenia tetrapedia</i>	—	—	—	—	—	0	—	—	+	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dicystosphaerium ehrenbergianum</i>	—	—	—	—	—	0	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Golenkinia radiata</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—
<i>Kirchneriella leunaris</i>	—	—	—	—	+	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lagerheimia longiseta</i>	+	+	—	—	—	0	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dacydium</i> sp.	+	+	+	+	+	0	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pediastrum simplex</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pediastrum duplex</i>	—	—	+	+	—	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—
<i>Scenedesmus bijugatus</i>	+	+	+	+	—	0	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	—	—	—
<i>Scenedesmus quadricauda</i>	—	—	—	—	—	0	+	+	+	+	—	—	+	+	+	+	+	+	+	+	—	—	—	—
<i>Scenedesmus acuminatus</i>	—	—	—	—	—	0	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—
<i>Eudorina elegans</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HETEROKONTAE																								
<i>Botryococcus braunii</i>	+	+	+	+	+	0	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
<i>Chlorobotrys regularis</i>	—	—	—	—	+	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
CONJUGATAE																								
<i>Spondylosium moniliforme</i>	—	—	—	—	—	0	—	—	—	—	+	—	—	—	+	+	—	—	—	—	—	—	+	+
<i>Staurastrum gracile</i>	+	+	+	+	+	0	+	+	+	—	+	+	+	+	+	+	—	—	—	—	+	+	+	+
PERIDINEAE																								
<i>Ceratium hirundinella</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Diplopsalis acuta</i>	—	—	—	—	—	0	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—
<i>Peridinium westi</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

+ Presence of organism
 — Absence of organism
 0 Samples not taken for technical reasons

Table II. (Cont'd)

	XI		XII		I		II		III		IV		V		VI		VII		VIII		IX		X	
	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G	T	G
ZOOPLANKTON																								
ROTATORIA*																								
<i>Ascomorpha saltans</i>							+	+							-	-	-	-	-	-				
<i>Anuraeopsis fissa</i>							-	-							+	+	+	+	-	-				
<i>Asplanchna brightwellii</i>							-	-							-	-	+	+	-	-				
<i>Brachionus budapestensis</i>							-	-							-	-	+	+	-	-				
<i>Epiphanes</i> sp.							-	-							+	+	+	+	+	+				
<i>Filinia longiseta</i>							-	-							+	+	-	-	-	-				
<i>Keratella cochlearis</i>							-	-							+	+	-	-	-	-				
<i>Keratella valga tropica</i>							+	+							+	+	+	+	+	+				
<i>Pedalia fennica</i>							-	-							+	+	+	+	+	+				
<i>Pedalia fennica oxyure</i>							-	-							+	+	+	+	-	-				
<i>Pedalia intermedia</i>							-	-							+	+	-	-	-	-				
<i>Platyas patulus</i>							-	-							-	-	-	-	+	+				
<i>Polyarthra remata</i>							+	+							+	+	-	-	-	-				
<i>Polyarthra vulgaris</i>							-	-							+	+	-	-	-	-				
<i>Synchaeta pectinata</i>							+	+							-	-	-	-	-	-				
CLADOCERA																								
<i>Diaphanosoma brachyurum</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+
<i>Bosmina longirostris</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>ceriodaphnia reticulata</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>ceriodaphnia rigaudi</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Daphnia lumholtzi</i>	-	-	-	-	-	0	-	-	-	-	+	+	+	+	-	+	-	+	-	-	-	-	-	-
COPEPODA																								
<i>Mesocyclops leuckarti</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Thermocyclops dybowskii</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nauplius</i>	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

* This list of species, determined by Berzins, is based on samples collected over the months of February, June, July and August only.

The Chroococcales show a distinct predominance over the Hormogonales, both in the number of species and in their seasonal distribution. Among the Chroococcales, *Microcystis flos aquae* is perennial, without, however, becoming dominant in the plankton at any time of the year. Another species belonging to this genus, *M. aeruginosa*, also a typical euplankton, has a limited seasonal distribution in the lake, being found in November and May.

Aphanocapsa pulchra, a species closely related to *Microcystis* taxonomically, is another perennial member of the plankton of Lake Tiberias, occurring generally in low numbers.

A minute blue-green alga belonging to this order is *Chroococcus minutus*, which appears in substantial numbers in every plankton collection. A second species, *C. limneticus*, a typical planktonic alga, was also occasionally recorded.

None of the several genera of Hormogonales appears to constitute an important element of the plankton. Such organisms as *Spirulina platensis*, *Anabaenopsis circularis* and *Lyngbia limnetica* have a sporadic occurrence, not always connected with the warm summer months.

In conclusion it may be said that the blue-green algae play only a limited role in the plankton of Lake Tiberias, the chief constituents of this group being some three species of Chroococcales which have a perennial existence.

DIATOMEAE

Diatoms are not very abundant in Lake Tiberias, although individual species are found in every collection. Seventeen species belonging to fourteen genera and six families were recorded in all.

Melosira granulata (Ehrbg.) Ralfs is by far the most common species. Two distinct varieties of this diatom were noticed: one, the more common, with a diameter of 16–20 microns, corresponding to the typical form of this species, and a second considerably less common and narrower one, with a diameter of 10–12 microns. The latter is *Melosira granulata* var. *angustissima* Müller. Both forms are characteristic of flat country and eutrophic waters in general.

In only one instance did a diatom, *Fragilaria crotonensis*, become so abundant as to cause a conspicuous water-bloom in the whole lake. This occurred during the month of January 1949. The organism appears occasionally as individual cells, but more frequently as bands or fan-like groups of varying numbers of cells. In this particular case this species definitely became the dominant element of the plankton. *Fragilaria crotonensis* is known to occur in the central European lakes during the summer, when the temperature of the water does not exceed 16°C. In our case, this species seems to have found a favourable habitat in Lake Tiberias just in the month of January, when the temperature of the water fluctuates between 14.5 and 15.5°C. During the three following months, i.e. February, March and April, the diatom appeared only occasionally in the plankton, although in these months, too, the temperature of the lake water did not exceed 15–16°C.

Other diatoms found among the net plankton in the winter months were *Gyrosigma acuminatum*, *Surirella ovalis* and *Cymatopleura solea*. In summer the presence of *Synedra ulna*, *Gomphonema* sp. and *Cymbella affinis* was recorded. Another diatom which, although only rarely recorded in the net plankton, formed a constant and important element of the food of cichlid fishes is *Amphora ovalis*. To a lesser extent, the same is also true of *Synedra affinis*.

A considerable number of diatom species recorded by us in Lake Tiberias have been identified by Rayss in Lake Huleh (1951). Among these species, *Melosira granulata*, *Synedra ulna*, *Amphora ovalis* and *Cymatopleura solea* are noted. This tends to show the influence of the River Jordan and Lake Huleh on the plankton of Lake Tiberias, and it is not impossible that additional species of diatoms and other groups recorded by Rayss in the same paper (1951) and not found by us in the present collection may eventually be found in Lake Tiberias as a result of further and more extensive work.

CHLOROPHYCEAE

The green algae are represented in the plankton of the lake by four orders, namely Protococcales, Volvocales, Tetrasporales and Ulotrichales. Of these, the Protococcales are by far the most important, comprising the largest number of species within this class. In all, 31 species of green algae were found, of which 28 belong to Protococcales grouped in seven families, the remaining orders being represented by one species each.

ORDER PROTOCOCCALES

FAMILY CHARIACEAE. The family is represented by one genus in the lake, *Characium*, which appears as epizootic upon the telson and appendages of copepods and occasionally on rotifers. At times it has also been observed in a detached condition, probably due to frictional causes. Two species were recorded, *Characium debaryanum* with oval cells and hyaline stalk and living on appendages of copepods, and *Characium hookeri*, with longer and elliptical cells and long stalk.

FAMILY HYDRODICTYACEAE. The family is represented in Lake Tiberias by the genus *Pediastrum*, which is one of the most common components of the plankton throughout the year. Both *Pediastrum simplex* and *P. duplex* appear regularly in practically every plankton collection, the former in larger numbers which reach a peak in the month of August. *Pediastrum duplex* was not found at all in the September, October and December samples, indicating a temporary disappearance of the organism during this season. Of the *Pediastrum* species listed in the systematic account, *P. tetras* was found only in the stomach contents of cichlid fishes.

FAMILY OOCYSTACEAE. The most conspicuous representative of this family is *Ankistrodesmus longissimus*, which is also a constant element of the plankton of Lake Tiberias. It has a long and slender body, slightly curved and attenuated at the ends. It attains a length of 500 microns and a width of 6 microns. It is never abundant, but one never fails to detect it in every plankton collection from the lake. Another species, *Ankistrodesmus falcatus*, which is common in shallower bodies of water and fish ponds, is only occasionally found in the plankton of the lake. The well-known genus *Oocystis* is represented in the plankton by at least one species. However, it almost always appears as mere traces, making it often difficult to detect, but it is as much a constant element of the plankton as some of the most common species of Protococcales present in the lake. The same is true of *Lagerheimia longiseta* and *Tetraëdron muticum*, which are found in small numbers in almost every plankton sample taken from the lake.

FAMILY SCENEDESMACEAE. The genus *Scenedesmus* is represented by a number of species, of which the most important are *S. quadricauda* and *S. bijugatus*. While the first species is present in all types of inland waters, being truly cosmopolitan in its distribution, the second occurs in the plankton of Lake Tiberias to a far greater extent than in that of fish ponds in the immediate vicinity of the lake and in the Jordan Valley in general. *Scenedesmus alternans* occurs in two forms, one, α -*seriatus* in which the smooth-walled ovoid cells are arranged in a single series, and a second, β -*alternans*, in which there is a very marked alternate arrangement of the component cells. The second form seems to be the more common in the plankton of the lake.

FAMILY COELASTRACEAE. The genus *Coelastrum* is represented by three species, of which *C. microporum* is the more common. This species was chiefly recorded in the plankton of the spring months.

FAMILY MICRACTINIACEAE. The only species of this group encountered during

The plankton analysis was *Golenkinia radiata*. This species, which is an important element of the phytoplankton of fish ponds of low salinity in the adjoining Beisan Valley (Komarovsky 1953), has only a very restricted seasonal distribution in Lake Tiberias (see Table II).

ORDER VOLVOCALES

FAMILY VOLVOACEAE. The only representative of this family found by us in our collections was *Eudorina elegans*, encountered only once off Ginossar in March 1949.

CONJUGATAE

The Conjugatae are represented in the plankton of Lake Tiberias by one family only, namely the Desmidiaceae. By far the most common species of desmids is *Staurastrum gracile*, which is perennial in its distribution, occurring in fairly large numbers both in the plankton samples as well as in the food of the plankton-feeding fish of the lake. A second species, *S. muticum*, has been occasionally recorded by us in the course of this investigation. *Spondylosium moniliforme* is another desmid found occasionally in the lake plankton, as well as in the stomach contents of *Tilapia nilotica* and other related species.

The poor representation of the desmid flora in Lake Tiberias is worthy of consideration. When one bears in mind that desmids thrive best in waters poor in calcium and with a slightly acid pH, one can easily see that Lake Tiberias is not the ideal environment for the development of this type of flora (Pearsall, 1932). The pH of the lake's water is around 8 and the calcium content is also relatively high. These conditions would, therefore, favour the development of diatoms rather than of desmids, as the results of this investigation confirm. The three species of desmids mentioned above present in the lake plankton are actually characteristic alkaliphile forms of this group of algae.

DINOFLAGELLATAE

The Dinoflagellatae are amply represented in the plankton of Lake Tiberias. Six species were recorded in all, of which the most important are *Peridinium westi* and *Ceratium hirundinella*.

Peridinium westi, which belongs to the section *Cleisto-Peridinium* of this genus on account of its circular outline as seen in the front view, is perennial in its distribution in the lake, although subject to seasonal fluctuations. Beginning in February, the organism forms veritable water-blooms comparable to those caused by blue-green algae in fish ponds (Komarovsky 1951) and constitutes the dominant element of the plankton. These blooms persist for three to four months, during which time the lake water assumes a yellow-brown colouration, which begins to subside in intensity only at the end of May or in June. According to information received by the author on this subject, this dinoflagellate causes similar blooms at this time of the year in fish ponds of the northern Jordan Valley, whose water supply comes from the Jordan River.

In view of the difficulties encountered so far in the identification of this organism a detailed morphological description is given below.

Peridinium westi has six apical plates in the epitheca, of which two are dorsal two median and two ventral. This arrangement of the plates can be seen in the following camera lucida drawings. The apical plates are surrounded by 7 precingular plates and a seventh apical plate on the ventral side touches the first and seventh precingular ones as is characteristic of all species of *Peridinium* belonging to the *Orthoperidinium* group, which comprises all fresh water forms. The hypotheca is made of 5 postcingular plates and 2 antapical ones. The length of the cells is 40–48 μ and the width 38–44 μ . *Peridinium westi* is known from central and northern Europe and from Africa (Lake Victoria) (Huber-Pestalozzi 1950).

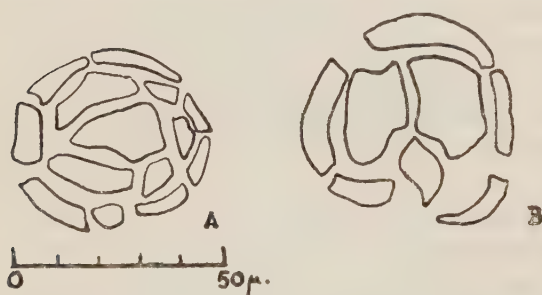


Figure 3
Peridinium westi Lemm. A. Epithecium
B. Hypotheca (plates separated along
the sutures due to treatment with Eosin
de Javelle)

The second species of *Peridinium*, namely *Peridinium bipes*, belongs to the *Poroperidinium* section of the genus owing to its angular outline. This species is somewhat less common in the plankton than *Peridinium westi*, although often found in the stomach contents of *Tilapia* species and *Acanthobrama terrae-sanctae* from Lake Tiberias.

Ceratium hirundinella, although present in the lake plankton throughout the year attains higher numbers in spring and summer. Its greatest abundance coincides with that of *Peridinium cinctum*, namely in March–April, thenceforth gradually decreasing in occurrence. It shows slight changes in the body form during the year. In May the organism is slightly longer and its antapical horns are more spread out than in winter. It also shows a tendency to develop a small third antapical horn. This characteristic disappears again in the following months, when the organism returns to its original size with the antapical horns closer together.

In addition to the variations of a seasonal nature, a special study has been made of the variation in general shape and size of this species in view of its pronounced plasticity, which is probably related also to specific conditions existing in different aquatic environments (Birti, 1955).

Several investigators have attempted to define definite types of *Ceratium hirundinella* according to certain well-defined characteristics, such as the number of antapical horns, total length and the position and angle of diversion of these horns in relation to the apical horn (Zederbauer 1904, Bachmann 1911, Schillang, 1913, Schroder 1918).

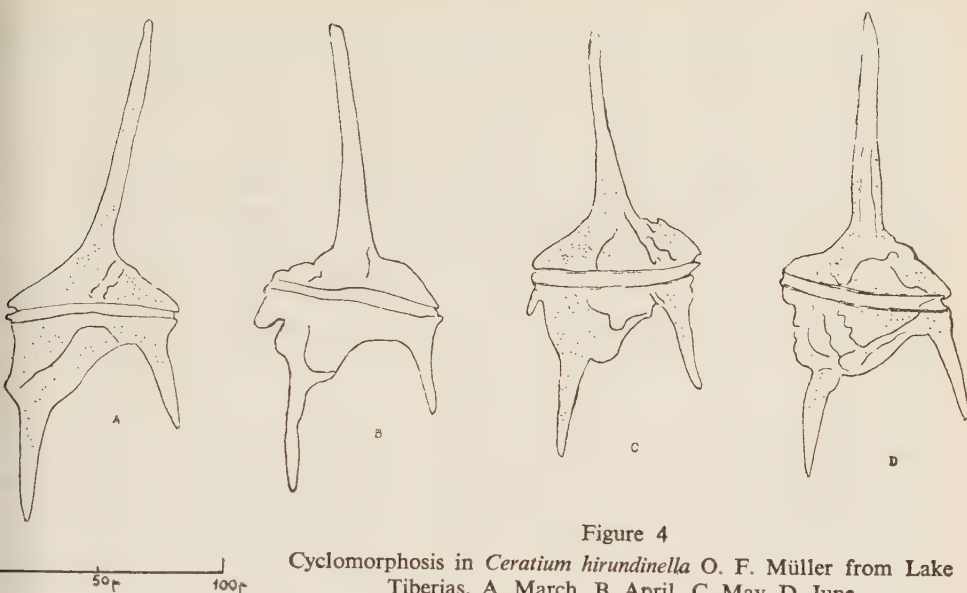


Figure 4
Cyclomorphosis in *Ceratium hirundinella* O. F. Müller from Lake Tiberias. A. March, B. April, C. May, D. June

Huber-Pestalozzi 1950). These investigators, however, based their studies on central and north European *Ceratia* and for this reason the type or types of *Ceratium hirundinella* present in Lake Tiberias are not easily fitted into any of the patterns proposed by them.

Yet, according to Schroder and Huber-Pestalozzi's key (1950, p. 263) and Schiller's description of the freshwater *Ceratia* (1937), we found the most common form of this species to be the *Brachyceroides* type, which comprises specimens with the antapical horn bent slightly inwards or almost parallel with the apical horn, of average total length of 120–150 μ and a diameter of the cell (t) of between 50–55 μ . This form was recorded in our material from almost all samples in which *Ceratium hirundinella* was present.

Another form, shorter and plumper, with distinctly divergent posterior horns and a protuberance below the girdle that could be interpreted as an incipient third posterior horn, accords well with the *Austriacum* type described in the above-mentioned sources. The diameter of the girdle in this form is in all cases above 50 μ , while the total length of the specimens reaches about 155 μ .

A form similar to the *Austriacum* type except for the absence of the reduced third posterior horn accords well with the *Carinthiacum* type.

There are, however, many transitional forms between these types, which makes clear-cut distinction between the afore-mentioned ones rather difficult, especially when we take into consideration the seasonal changes in body form so frequent in this species. Other irregular features in the *Ceratia* of Lake Tiberias are the presence of acute protuberances occurring alternately either on the outside of the longer

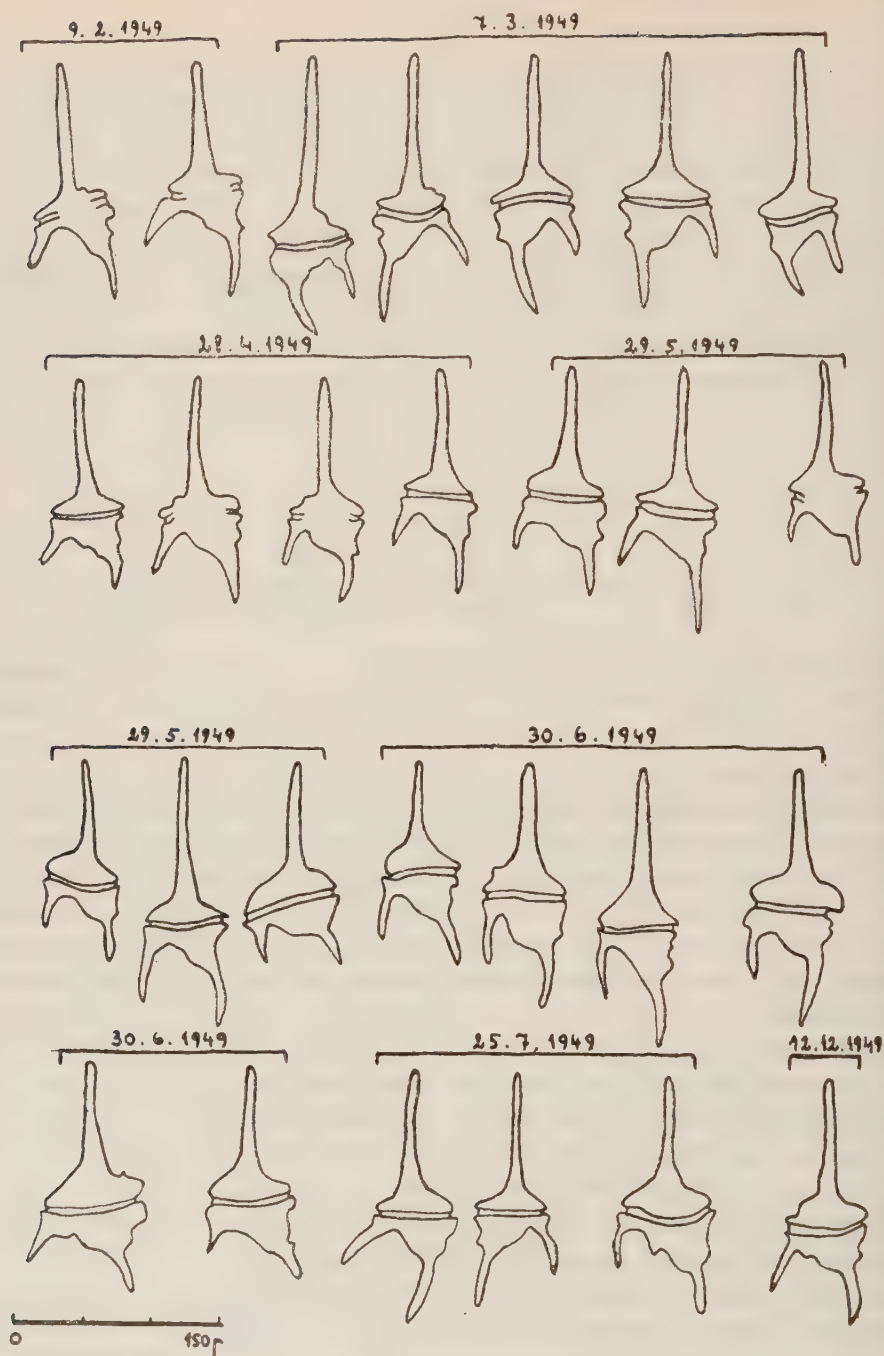


Figure 5

Local variations in populations of *Ceratium hirundinella* O. F. Müller at different times of the year

posterior horn and quite separate from the stump protuberance below the girdle, or on the lower part of the cell between the two horns.

In rare cases abnormal forms with cleft posterior horns were also recorded. (Plate I, 3). In order to present a better picture of the great variability of body forms of *C. virundinella* in Lake Tiberias at various times of the year, a series of camera lucida drawings is given, including among other forms, those described above, as well as some of the transitional and less well-defined forms and irregularities of structure. The species was previously recorded in the plankton of Lake Tiberias by Huber-estalozzi (1951) and Rayss (1951).

The three remaining species of dinoflagellates listed in the systematic list of plankton organisms occur only in low numbers in the plankton.

The zooplankton

The zooplankton of Lake Tiberias was described by Annendale (1913) as neither abundant nor conspicuous in any way. In his words, "It consisted for the most part of a few species of minute copepods and rotifers, only a few species of each group being represented."

Gurney (1913) also described the zooplankton from Lake Tiberias as being uniform in its composition, and gave a list of the Entomostraca found by him in the Lake. He listed in his work four species of Cladocera from the plankton, apart from a fifth one mentioned by Annendale as occurring in deeper water and one species of Copepoda, the individuals of which were mostly immature. The same author also stressed the uniformity of the zooplankton in this lake throughout the years from the data provided by Barrois, Annendale and himself. The same view is held by Brehm (personal information), who examined collections of Cladocera sent to him by the author.

ROTATORIA

The rotifers collected in the course of this investigation were examined and identified by Dr. B. Berzins from Lund, Sweden, to whom a collection of samples taken during February, June, July and August 1949 were sent by the author. Fifteen species were found by him in this material, some of them occurring in large numbers. Among the latter he found *Keratella valga tropica* to be common during the summer months, especially August, *Pedalia fennica* during July and *Synchaeta pectinata* abounding during February. Since the samples examined by Dr. Berzins did not represent a complete annual cycle, it is possible that the plankton includes additional species, although it can safely be stated that the list submitted by the Swedish scientist comprises the most common forms present in the lake.

The Rotatoria of Lake Tiberias as a group have been studied by several investigators. Barrois (1894), who reported five species of rotifers from the lake, stressed the occurrence of members of this group in the upper water layers, between 3-4 m deep. As an exception he mentions *Asplanchna syrinx*, which was found by him at the

10 m depth, although quite rare. In a later survey of the fauna of Lake Tiberias, Annendale (1913) listed seven species of Rotatoria, none of which, in his opinion, had any geographical interest. He further stated that "the rotifer fauna, indeed, seems to be poor compared even with that of other lakes in Syria and Palestine, and all the forms as yet recorded belong, according to Harring (1913), to well-known and widely distributed species." He also considered *Brachionus patulus militaris* as the most important rotifer species in the lake. This organism was also found by Rousselet (1913) in abundance, at the surface of the lake, both by day and by night.

More recently, Wirszubski (1944) stressed the uniformity existing in the composition of the rotifer fauna of Lake Tiberias. In his view, this uniformity is brought about by the strong winds that blow over the lake, mixing the top layers of the water, as well as by the stable environmental conditions prevailing in this lake. Some changes, however, were observed by this author in the rotifer fauna of the shore waters and those affected by the inflow of the Jordan River in the northern region of the lake and along its bed.

CLADOCERA

The Cladocera are represented in the plankton of Lake Tiberias by five species, four of which are truly eupelagic, while the fifth is associated with greater depths of the lake. Two additional species mentioned in the systematic account, namely *Alona affinis* and *Chydorus sphaericus*, have been recorded by the author (1952) in the stomach contents of *Acanthobrama terrae-sanctae* of Lake Tiberias. These species are considered by Barrois (1894) to be deep-water forms which are never caught in the plankton samples during the day.

A single female specimen of *Moina rectirostris* was also found by Prof. Brehm in the material of this collection. He considers its presence to be accidental in the plankton of Lake Tiberias, not previously found by other investigators (personal information).

When we compare the list of Cladocera species recorded in the course of this study with those provided by Barrois and Annendale, we see that no changes have taken place in the composition of the plankton during a period of over sixty years. This seems to indicate the stability in the biocenotic pattern of the zooplankton population, probably as a result of fairly constant ecological and hydrographic conditions prevailing in the lake. A similar view was taken by Baldi (1951), who compared the zooplankton populations of Lago Maggiore over a period of 40 years.

The seven species and one variety mentioned in the systematic account belong to four families: Sididae, Bosminidae, Daphniidae and Chydoridae.

FAMILY SIDIDAE. The sole representative of this family in the plankton of Lake Tiberias is *Diaphanosoma brachyurum*, which is probably identical with *Daphniella brachyura* as described by Barrois (1894). It is the largest species of Cladocera in this lake, the females often reaching 700 microns in length. It is present in the plankton

throughout the year; egg-carrying females have been observed during the months of February and July. The species is easily recognised by its perfect transparency, its head without a rostrum and the special structure of its antenna, the exopodite of which consists of two segments. It is a truly eupelagic organism which, according to Barrois (1894), is abundant chiefly between the 3 and 10 m depths. At 25 m it is already rare and at 40 m is very rare indeed.

FAMILY BOSMINIDAE. The species representing this family in Lake Tiberias is *Bosmina longirostris*, accompanied by *B. longirostris* var. *cornuta*. Both the main species and the variety are very common in the plankton throughout the year, chiefly in the upper layers of the water. Barrois found this species in greatest abundance between 3 and 5 m deep; it was quite rare at the surface and at the 10 m depth and below. *Bosmina longirostris* is probably the most abundant cladoceran in Lake Tiberias and is one of the conspicuous organisms of the plankton. Its size reaches about 0.5 mm in length, usually less; it is entirely transparent, like most other limnetic Cladocera, and is easily recognised by the distally-increasing row of small spines present at the base of its claw. The end segment of the claw is also provided with small teeth. The organism attains the peak of its abundance in summer, although it is perennial in the plankton of the lake (this applies equally to the main species and the variety).

FAMILY DAPHNIIDAE. This family is represented in the plankton by two species of *Ceriodaphnia*, *C. reticulata* and *C. rigaudi*, the first being the more common. *Ceriodaphnia reticulata* has its claw provided near the base, with 3-7 rough teeth which form an easy sign for the identification of the species. The reticulate pattern of its transparent capsule is also a characteristic feature of this organism. It reaches a peak of abundance during February and March. *Ceriodaphnia rigaudi* is easily distinguished from the former species by a horn-like process on its head. Both these species are, according to Barrois, characteristic of deeper layers of water, from 10-20 m, a fact which has been confirmed by our own findings.

Another species belonging to this family is *Daphnia lumholzi*, which is always associated with deeper layers of water near the lake bottom, being found only very rarely in the upper layers. It is recognisable by its helmet, which is subject to the phenomenon of cyclomorphosis. The species was recorded from the month of April until July.

FAMILY CHYDORIDAE. The two species of Chydoridae recorded in the lake, *Alona affinis* and *Chydorus sphaericus*, as mentioned above, are classified as deep-water forms, as they are never caught during the day catches. An indication of the presence of these species in the lake was provided by their occasional occurrence in the stomach contents of *Acanthobrama terrae-sanctae* (Komarovskiy 1952), in fish specimens collected near the inflow of the River Jordan into the lake on the latter's northern shores.

COPEPODA

The Copepoda from this collection were examined and identified by Dr. K. Lindberg, of Lund, Sweden. This group is found in large numbers in the lake plankton throughout the year, constituting the greatest part of the zooplankton. The two species recorded are *Mesocyclops leuckarti* Claus and *Thermocyclops dybowskii* Lande.

Whereas the first species, *Mesocyclops leuckarti*, has a world-wide distribution, being recorded in lakes of all five continents, the second, *Thermocyclops dybowskii*,

is limited solely to the subtropical regions, such as Afghanistan, Turkestan, Mesopotamia and North Africa, especially Egypt and Ethiopia (Gurney 1933).

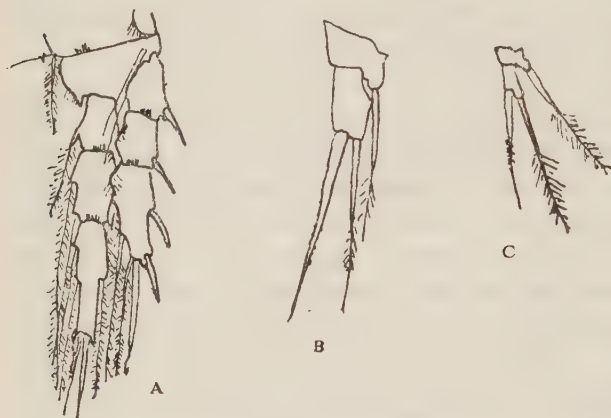


Figure 6

Mesocyclops leuckarti Claus. A. Leg 4 (Lake Tiberias). C. Leg 5. *Thermocyclops dybowskii* Lande, B. Leg 5 (Palestine) — after Gurney, 1933

Both species belong to the subgenus *Mesocyclops*, which was, however, revised by Kiefer (1928, 1930). Kiefer divided it into two subgenera: *Mesocyclops s. str.* and *Thermocyclops* Kiefer. According to this author, the distinguishing character is the position of the inner seta or spine on leg 5. In the former it is on the inner side, near the apex, while it is apical in the latter. The species of *Mesocyclops s. str.* are, on the whole, larger and stouter, while those of *Thermocyclops* are of more slender built and more often limnetic.

Gurney does not consider these characteristics important enough to separate the two subgroups (1933). In our view, however, the two species mentioned above are clearly distinguishable according to Kiefer's description and we therefore tend to accept his classification as such, although it is not our intention to debate within the framework of this paper the systematic issue involved.

Mesocyclops leuckarti is subject to local variations in body form. These variations are morphological adaptations to the particular water habitat where this copepod is found. These variations in body form have been studied by Gurney (1933) and are significant enough to distinguish between the various forms considered by him.

THE VERTICAL DISTRIBUTION OF THE PLANKTON

As mentioned above, the author had the opportunity of examining for their plankton content water samples collected during May and June 1950, in the course

of the special investigation referred to above (results summed up in De Leeuw 1950; De Leeuw and Auerbach 1951, Oren 1957). In this way the vertical distribution of the main plankton components was established for this time of year, when the summer stagnation, according to the latter author, is already complete and the thermocline is situated between 15–20 m. The stations from which plankton material was examined were (see contour map of Lake Tiberias, Figure 1):

Station No.	Date	Coordinates		Depth (m)
		N	E	
II	26.V.50	243.9	208.5	31.50
IV	28.V.50	243.2	201.9	21.50
VI	28.V.50	243.0	203.8	30.00
XXII	29.V.50	242.9	205.3	35.00
XXVI	29.V.50	241.7	201.8	12.50

Water samples of 100 cc each were taken from the Nielsen reversing bottles, which operated at 5 m intervals at depths ranging from the lake surface down to the bottom. An adequate quantity of formalin was added to these samples in order to obtain a concentration of 4%. The plankton thus obtained was examined solely for the species composition and no actual counts of specimens were made.

Table III sums up the phytoplankton and zooplankton species found at the various depth levels at the above stations.

The results of the plankton examinations made at various depths from the above stations indicate the existence of a more or less uniform distribution up to a depth of 20 m. The abrupt drop in the general number of species, which is probably reflected also in the actual number of specimens below the 20 m depth level, confirms the existence of the thermocline which, according to Oren (1957), is situated at about 17 m by this time of the year, separating the epilimnion from the oxygen-deficient hypolimnion. For a true appraisal of this phenomenon, however, the phytoplankton and the zooplankton must be considered separately.

The plankton algae show a more or less uniform distribution in the whole water column from the surface down to the thermocline level. This is true of most algal species recorded in these samples and especially of those belonging to Protococcales, Chlamydomonadaceae and Peridineae groups, which form by far the most important part of the phytoplankton. Below the thermocline, only sporadic specimens of a few species, probably better adapted to a state of oxygen deficiency, were found at depths reaching 35 m. Some of these organisms were found in an unhealthy condition due to the abnormal environmental conditions in which they lived.

TABLE III
Distribution of plankton organisms at various depths in Lake Tiberias, May 1949

Species	Depth in metres							
	0	5	10	15	20	25	30	35
PHYTOPLANKTON								
<i>Ankistrodesmus falcatus</i>		+						
<i>Ankistrodesmus longisimus</i>	+	+	+	+	+	+	+	+
<i>Botryococcus braunii</i>	+	+	+		+		+	+
<i>Ceratium hirundinella</i>		+	+					
<i>Characium debaryanum</i>					+			
<i>Chroococcus minutus</i>			+	+				
<i>Chroococcus turgidus</i>	+	+	+	+	+			
<i>Coelastrum microporum</i>				+	+			+
<i>Crucigenia tetrapedia</i>	+		+	+				
<i>Cymbella affinis</i>	+				+			
<i>Diplopsalis acuta</i>		+	+					
<i>Dictyosphaerium pulchellum</i>	+							
<i>Euglena acus</i>				+				
<i>Glenodinium cinctum</i>	+							
<i>Golenkinia radiata</i>		+	+	+	+			
<i>Kirchneriella</i> sp.		+						
<i>Lagerheimia longiseta</i>	+	+	+	+	+		+	
<i>Lyngbia cryptovaginata</i>	+							
<i>Melosira granulata</i>		+	+	+	+			
<i>Merismopedia glauca</i>	+	+			+			
<i>Microcystis flos aquae</i>	+	+	+	+	+	+	+	
<i>Navicula</i> sp.			+		+			
<i>Oocystis</i> sp.	+	+	+	+	+	+		
<i>Oscillatoria constricta</i>	+		+		+		+	+
<i>Pediastrum simplex</i>	+	+	+	+	+	+	+	+
<i>Pediastrum tetras</i>		+	+	+	+			+
<i>Peridinium westi</i>	+	+	+	+	+	+	+	+
<i>Poroperidinium</i>	+	+	+	+	+			
<i>Scenedesmus bijugatus</i>	+	+	+	+	+			
<i>Scenedesmus quadricauda</i>	+		+	+	+		+	+
<i>Spirulina platensis</i>					+			
<i>Spondylosium moniliforme</i>	+	+	+	+	+	+		+
<i>Staurostrum</i> sp.	+	+	+	+	+			
<i>Tetraedron muticum</i>	+	+	+					+
ZOOPLANKTON								
<i>Actinophrys</i> sp.			+					
<i>Vorticella</i> sp.		+	+	+				
<i>Anuraea</i> sp.					+			
<i>Asplanchna brightwelli</i>			+	+				
<i>Brachionus budapestensis</i>			+					
<i>Polyarthra</i> sp.		+						
<i>Bosmina longirostris</i>			+	+	+			
<i>Ceriodaphnia reticulata</i>			+		+			
<i>Mesocyclops leuckarti</i>		+	+	+				
<i>Thermocyclops dybowskii</i>				+	+			
<i>Nauplius</i>		+	+	+				

As far as the zooplankton is concerned, the same general trend in its distribution could be observed. Representatives of the main zooplankton groups were found at the various depths from 5 m down to the 20 m depth level, while no specimens whatsoever could be detected at lower depths. No implication is made, however, that the zooplankton is absent from 0–5 m, as no samples were taken between these levels; it can only be said that the main zooplankton components were absent from the water layer just below the surface from which the 0 sample was taken, probably as a result of the strong sun-action prevailing during the morning hours. This seems to indicate that the oxygen deficiency of the hypolimnion, which, according to Oren (1957), reaches its height in June and the following summer months, is responsible for the absence of any pelagic animal life in this part of the lake and causes the concentration of animal life in the oxygen-rich epilimnion.

In the case of planktonic algae, the reason for their poor representation in the hypolimnion during the summer lies not only in the presence of a thermocline but also in the low visibility of the lake, which causes them to concentrate chiefly in the upper layers of the water.

DISCUSSION AND CONCLUSIONS

One of the first things that demand consideration in the light of the data presented in the preceding sections is the attempt to place Lake Tiberias into one of the accepted patterns of lake classification.

One of the best-known systems proposed in this connection is that of Thienemann (1931), who introduced the notions of oligotrophic and eutrophic, to which Naumann (1929, 1931), working simultaneously, added a third, the dystrophic. These notions relate chiefly to the productivity characteristics of the various lakes, oligotroph implying low productivity, eutroph implying high productivity and dystroph a rather aberrant type rich in humic material.

If the physical, chemical and biological features of Lake Tiberias on the basis of the available information are checked against the condensed table drawn up in the Thienemann-Naumann classification of oligotrophic, eutrophic and dystrophic lakes (Welch 1935), it soon becomes clear that this lake does not fit entirely into any of these types. Indeed, some of the characteristic features of Lake Tiberias fit into the oligotrophic type, others, perhaps the majority, into the eutrophic type, and still others into neither of these. This indicates that this well-known system of lake classification cannot be applied universally, especially in the case of tropical and subtropical lakes. The same conclusion was reached by Hofstede (1955) on the basis of available data while carrying out a survey and appraisal of the fishing resources of Lake Tiberias.

A somewhat more detailed examination of these characteristics in regard to the Thienemann-Naumann classification would perhaps be appropriate at this point.

TABLE V

Selected physical, chemical and biological characteristics of Lake Tiberias in the light of the Thienemann-Naumann classification of lake types

Characteristics	Oligotrophic type	L. T.	Eutrophic type	L. T.	Dystrophic type	L. T.
General form relations	Deep; shoals narrow or absent; hypolimnion > epilimnion	+	Shallow; shoals broad; hypolimnion < epilimnion	—	Deep to shallow in bog surroundings or old mountains	+
Colour of water	Blue to green; characteristic colour always predominant	—	Green to yellow and brownish green; characteristic colour often concealed by vegetation colour	+	Yellow to brown; characteristic colour always predominant	+
Transparency	High	—	Lower; eventually very low	+	Low	+
Suspended detritus and deep deposits	Minimal quantities	—	Large quantities	+	Humic materials abundant	+
Dissolved oxygen content	Uniform from surface to bottom; abundant in hypolimnion; few or no putrefactive processes	—	In deep lakes of this type O ₂ content in thermocline strongly increased; little or no O ₂ in hypolimnion; putrefactive processes	+	As in eutrophic type	+
Littoral plants	Scanty	+	Abundant	—	Scanty	+
Plankton	Water bloom rare; Chlorophyceae and to some extent the diatoms dominate over the Schizophyceae	— ±	Water bloom abundant; Schizophyceae, Diatomeae, Chrysomonadales and the Peridineae predominate	+	Water bloom absent or very rare; Schizophyceae and diatoms, Chlorophyceae, Chrysomonadales, Peridineae, Desmidiaceae present	— +
Profundal fauna						
a. Qualitative	Rich in species; requiring high O ₂ content	—	Poor in species; with wide toleration of O ₂ content changes; Chironomus fauna	+	Still poorer in species; wide toleration of O ₂ content changes; Chironomus fauna poor	+
b. Quantitative	Relatively rich	—	Rich	—	Poor	+
Qualitative correlation between plankton and profundal fauna	Present	—	Absent	+	Bottom fauna always poor; Phytoplankton poor; zooplankton often rich	—
Deep-dwelling coregonine fishes	Abundant	—	Present only in exceptional cases	—	Always absent in advanced dystrophic lakes	+

It can be seen from this table that oligotrophic, eutrophic and sometimes dystrophic characteristics are intermingled in the case of Lake Tiberias. Such typically eutrophic characteristics as the colour of the water, low transparency, hypolimnion with a low or entirely absent oxygen content during the summer, and the occurrence of water blooms are matched with equally typical oligotrophic features, such as relatively great depth, narrow shoals and a relative predominance of Chlorophyceae and Diatomeae over Schizophyceae.

At the same time it is possible that if the characteristics of this lake were examined against the background of similar bodies of water situated more or less within the same subtropical belt on both sides of the equator in Asia and North Africa, a nearer and better-defined basis for their classification might eventually be found. Even Thienemann (1931), aware of the wide discrepancies occurring in the case of the

so-called eutrophic lakes in tropical regions, suggested their further subdivision into more specialised types such as alkalitrophic, siderotrophic or acidotrophic, according to their respective characteristics.

From the point of view of the distribution of species, Lake Tiberias proves to be a meeting ground of typically temperate species characteristic of European and North American lakes on the one hand and tropical and subtropical ones on the other. As such, it may well be that Lake Tiberias forms, in some cases, the most southerly limit in the distribution of some northern and temperate species while in other cases it may form the most northerly limit in the distribution of tropical and subtropical species. No doubt, many such species, both of tropical and subtropical origin, would to a certain extent overlap in their geographical distribution with species of temperate origin, leaving no clear-cut line of distinction between the water areas they generally inhabit.

The phytoplankton of Lake Tiberias is characterised by a predominance of the diatom *Melosira granulata*, a large number of species of Protococcales of the green algae and some Chroococcales of the blue-green algae. Such an association of algal groups and individual species is similarly found in most East African lakes examined by Worthington and Ricardo (1936), and also recorded from the Nile and Nile Delta by Bachmann (1936) and Steuer (1942). Of special mention is also the small number of Desmidiaceae present in the lake, the species of which are probably characteristic of alkaline waters.

The coexistence of tropical or subtropical and temperate species in the plankton of this lake is also shown by the two species of Copepoda mentioned in this paper. Of these, *Mesocyclops leuckarti*, a typically cosmopolitan species is equally common in European as well as in many subtropical lakes, such as L. Rudolf, L. Edward, L. Bunyoni and L. Naivasha (Worthington and Ricardo 1936) in East Africa, whereas *Mesocyclops dybowskii* is characteristic of the subtropical regions of southern Asia and northern Africa. Another remarkable feature of the plankton of Lake Tiberias is the complete absence of Diaptomids among the Copepoda. While Diaptomids are fairly common in temperate lakes, as well as in fish ponds and their water sources adjoining Lake Tiberias, their absence from the plankton of this lake is again comparable to that of some of the East African lakes mentioned above (Worthington and Ricardo 1936). On the other hand, it could be assumed that the absence of the Diaptomids in the lake is due to ecological rather than geographical factors just because these copepods are found to be common in adjoining bodies of fresh water.

The same is true of the few species of Cladocera recorded from the plankton of Lake Tiberias, as for example the occurrence of *Diaphanosoma brachyurum* and *Bosmina longirostris*, characteristic also of temperate lakes, side by side with *Ceriodaphnia reticulata*, which is truly cosmopolitan, and *Ceriodaphnia rigaudi*, which is generally found in subtropical lakes only.

From all these data it appears that the plankton of Lake Tiberias, in spite of some very pronounced eutrophic characteristics of the lake as a whole, should be compared to that of lakes situated at similar or close latitudes in order to define more precisely the type to which it belongs. Special stress should be put on the lakes bordering the Mediterranean Sea both in the north and in the south, which should serve chiefly as a basis of comparison in the analysis of plankton characteristics. Reference should then be made to the composition and fluctuations of the plankton in the lakes of tropical and subtropical regions as a whole.

The vertical distribution of plankton species in Lake Tiberias is still to be studied. The data presented in this report refer only to the plankton stratification at a limited number of stations during the summer stagnation, although these stations represent an almost complete cross-section of the lake. The circulation periods existing in the lake suggest important problems of migration in the plankton communities which should be thoroughly investigated in relation to whole systematic groups and individual species. The plankton pulses occurring in the lake should also be studied at as large a number of stations as possible in view both of seasonal and local variations, as the results of such a study might be directly correlated with fisheries investigations. So would a study of the diurnal migration of the macroplankton which has not been attempted in the course of the present investigation.

It should also be pointed out that a thorough study of the nanoplankton of Lake Tiberias, preferably in a living condition, is necessary, not only to supplement our knowledge of the microflora and microfauna of this lake but also to obtain a better understanding of its productivity.

The available data should then be interpreted in the light of edaphic, climatic and morphometric conditions prevailing in this part of the world, with a view to arriving at a closer and more accurate characterisation of this lake.

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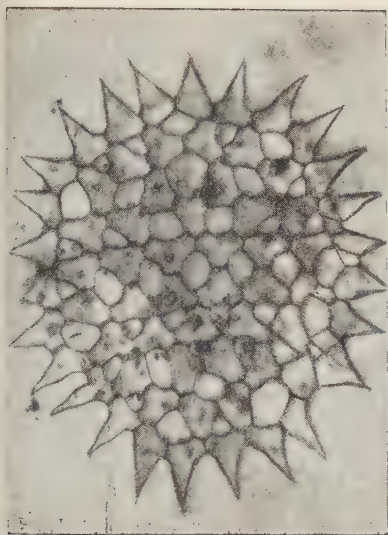
Thanks are due to the members of the boat crew at Lake Tiberias and of the local Fisheries Division Office for their cooperation in carrying out the field work.

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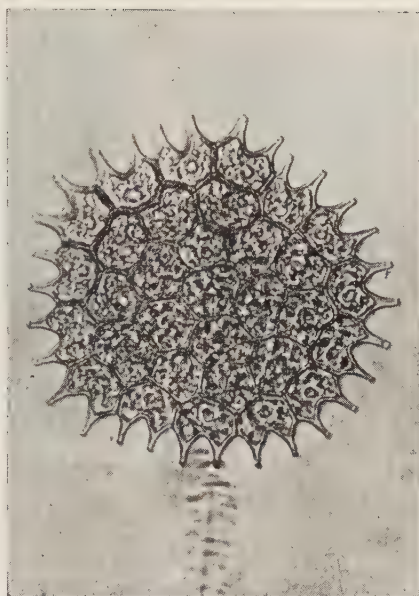
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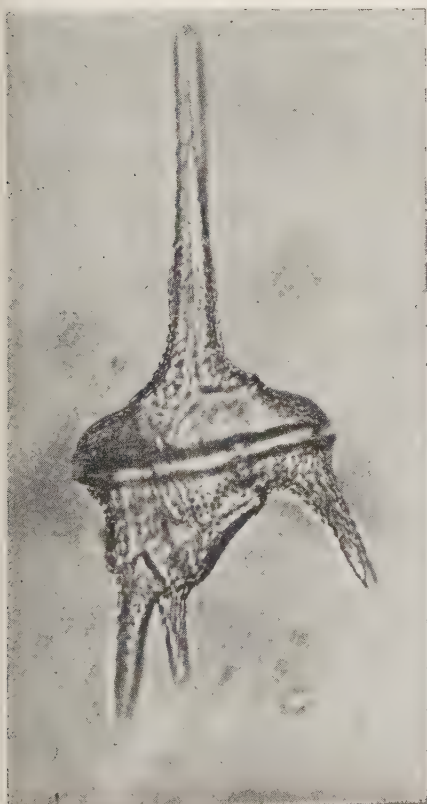
* Papers and works not referred to in the text or not available in the original.



1.



2.



3.



4.

1. *Pediatrum simplex*, $\times 400$.
2. *Pediatrum boryanum*, $\times 400$.
3. *Ceratium hirundinella*, $\times 600$ (abnormal form).
4. *Keratella valga tropica*, $\times 250$.



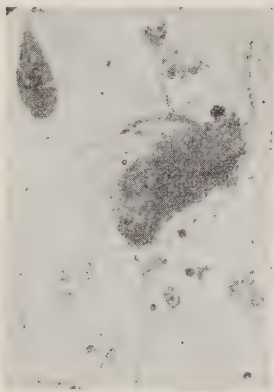
5.



6.



7.



8.



9.

5. *Keratella cochlearis*, $\times 300$.
 6. *Bosmina longirostris*, $\times 100$.
 7. *Diaphanosoma brachyurum*, $\times 40$.
 8. *Daphnia lumholtzi*, $\times 25$.
 9. *Thermocyclops dybowskii*, $\times 100$.

Plate II. Some characteristic organians from the plankton of Lake Tiberias.

LETTER TO THE EDITOR

A remark on vole outbreaks. F. S. BODENHEIMER, *Dept. of Zoology, The Hebrew University of Jerusalem.*

Some recent remarks in vole literature^{1,2} indicate doubts concerning the findings of Hamilton³ on *Microtus pennsylvanicus* and of the author⁴ on *M. güntheri* that at the beginning of a vole outbreak the number of young per litter was double the normal figure and the percentage of pregnant females higher than usual. A few words may be devoted to this complex phenomenon.

In our animal house the monthly average birth rate over 13 years of uninterrupted breeding of *M. güntheri* was fairly stable from year to year, except for a small but significant decrease in the number of litters, as well as in the number of young per litter, at the height of winter and summer, with an increase occurring in spring and in autumn (Ref. 4, p. 19). Hoffman¹ and Stein² did not observe a sudden increase of natality in nature and doubted its influence on vole outbreaks. In their observations on *M. californicus*, *M. montana* and *M. arvalis*, the natalities were more or less constant. They ascribed changes in vole abundance to the other factor in the balance, i.e. mortality, especially prenatal and infant mortality. Doubtless both eventualities occur in nature, either in different species or even in different seasons or years in the same species. We have never generalized, but only described what we observed in nature. These observations differed greatly from the relatively stable results of our normal breedings, which can, however, be experimentally influenced by feeding.^{5,6}

The next important point is that heightened natality need not persist for long in order to be effective. The outbreak involves increased litter size and number of litters as well as number of pregnancies. When the population in autumn rises from 2 per unit to 40, a twentyfold increase has occurred, and if this is followed, as occasionally happens, by a second period of spring natality increase to 200, only a fivefold but very much more conspicuous increase has taken place. These are the actual ranges of fluctuation observed by us in nature for *M. güntheri*. If such an increased natality lasts only 2 to 3 months under favourable conditions of weather, food, etc., this is quite sufficient, and there is no need for these conditions to continue throughout the entire increasing wave of the outbreak. Our regular findings in autopsies in the field in 1930 and eventually in other years of incipient outbreaks were 7 to 14 embryos per pregnant female, as compared with the 3 to 7 young per litter in normal times. In addition we observed a heavy rise in the percentage of pregnant females. These data explain the occurrence of an outbreak even if the period of heightened natality is a limited one. We⁷ have noted that the fluctuations are in the range of natural fertility of *M. güntheri*, in contrast to the stable natality of the laboratory.

We never presumed that this is the norm for all vole outbreaks, either as regards the outbreaks of all species or even in all cases of *M. güntheri* outbreaks. We have never denied the possibility that in other species, localities and conditions, a changed mortality may be the decisive factor, as claimed by Hoffman¹ and Stein². It seems unreasonable not to apply the same considerations to a different set of facts (not of interpretations!). Mortality is conspicuously the decisive factor in the collapse of outbreaks. But whether changes occur in the number of ovulations and embryo resorptions, in infant mortality for inner or environmental reasons, and so forth, is still far from clear. We have never ascribed a reduced rate of maturing adults solely to a lower ovulation rate.

Despite the rapidly growing accumulation of data on vole fluctuations, we are still only at the very beginning of reaching an understanding of their dynamics. It seems to us that unwise laboratory experiments or precocious applications of physiological theories (such as the extension of the well-based "stress" theory in man of Selye for short-term stress effects to long-term stress effects in nature,

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which offer so many possibilities for compensation phenomena) have a retarding rather than helpful effect on progress, especially insofar as the proponents of such claim generalized validity. The most deleterious factor is that every individual leaves his field-work after a very few years. We must find ways to make very prolonged observations possible and to agree upon the technique of observations to be applied in such long-term projects in order to ascertain whether all results are fully compatible with previous data.

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